The Diet and Nutritional Ecology of the Auckland Tree Wētā *Hemideina thoracica*

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Abstract

Insects are the main consumers of primary production in many terrestrial ecosystems, they are involved in the upwards migration of energy to higher trophic levels, and are often extremely important in structuring their ecosystems. Despite the many important ways that insects influence their ecosystems, many of the most basic aspects of the functional ecology of many groups of insects have not been investigated, and a great deal remains to be learned about what roles they play in the structure and functioning of their ecosystems. This study focuses on the Auckland tree wētā *Hemideina thoracica* (Orthoptera: Anostostomatidae, White, 1842), the most widespread species of tree wētā in the North Island of New Zealand, and one of the least studied species in the genus *Hemideina*.

Faecal fragment analysis revealed that the diet of a population of *Hemideina thoracica* from a mixed podocarp/broadleaf forest was composed primarily of the leaves, fruits, and seeds, of the native plants *Prumnopitys taxifolia, Podocarpus totara, Dacrycarpus dacrydioides, Kunzia ericoides*, *Melicytus* sp., *Pennantia corymbosa*, and *Coprosma rotundifolia*, but the consumption of other invertebrates was also common, and formed a smaller component of the overall diet. *Hemideina thoracica* were also shown to feed selectively while foraging. It was determined that some plants were eaten readily by the wētā when encountered, while other plants that were equally abundant were either not consumed, or were consumed far less than would be predicted by their availability. Performing a solvent extraction, using hexane, revealed that the concentration of lipids and oils in the leaves of preferred plant species was higher than in the leaves of non-preferred species, and *Hemideina thoracica* may preferentially consume plants that have high lipid concentrations in their leaves. It also appeared probable that they forage on the forest floor more frequently than has been previously recognised.

A nutritional analysis performed in captivity revealed that *H. thorac*ica are capable of balancing their consumption of the macronutrients protein and carbohydrates to construct an optimal diet from one or more sub-optimal sources, and strongly regulate their consumption of protein. When presented with the opportunity to construct their own diet, they consumed significantly more carbohydrates than protein, and constructed a diet with a mean protein to carbohydrate ratio of 27:73. They digested carbohydrates more efficiently than

protein, but converted the protein that they consumed into biomass with a very high level of conversion efficiency. These results supported the results of the fragment analysis by demonstrating that the natural, optimal diet of *H. thoracica* is most likely composed of carbohydrate rich foods, but they may also be naturally omnivorous, as they utilise protein very efficiently.

The third, and final experiment, investigated whether *H. thoracica* feed on fruit in a manner that may facilitate seed dispersal for native plants in the wild. This experiment involved feeding fruit from three different native plants, *Coprosma repens*, *Cordyline australis*, and *Fuchsia procumbens* to a group of 40 *H. thoracica*, and revealed that *H. thoracica* frequently consume the flesh of the berry from around the seed, without ingesting the seeds themselves. When the seeds were consumed, 100 % of them were destroyed by the wētās digestive process, even in the case of very small and numerous seeds, like those of *F. procumbens*. It is therefore highly unlikely that *H. thoracica* is a seed dispersing plant-mutualist, as the seeds are either left where the fruit had fallen, or are destroyed.

The combined results of these studies demonstrated that *Hemideina thoracica* is an omnivorous polyphage, and their wild diet is composed primarily of leaves, fruits, and seeds, and the concentration of lipids and oils in the leaves appears to be an important cue in determining the palatability of different species. They are also naturally omnivorous, and protein derived from eating other insects is a common component of their overall diet They have a well developed ability to balance their consumption of protein and carbohydrates, and self-select a carbohydrate rich diet in captivity. It is also extremely unlikely that that *H. thoracica* act as seed dispersers for native, fruit producing plants.

Keywords: Wētā, *Hemideina thoracica*, selective foraging, nutrient balancing, seed dispersal.

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1.1 Introduction

1.1.1 The Tree Wētā

Tree wētā are large bodied, flightless, nocturnal insects, and an iconic component of the fauna of New Zealand. Tree wētā are grouped in the Order Orthoptera, which also includes the grasshoppers (Acrididae, MacLeay, 1918), crickets (Gryllidae, Laicharding, 1781), and katydids (Tettigoniidae, Kraus, 1902) with whom wētā share many basic morphological traits like cylindrical bodies, elongated hind legs, and mandibulate mouthparts. The Order Orthoptera is divided into two suborders, the Ensifera and the Caelifera. The Ensifera are considered the more ancient of the two and first appears in the fossil record in the carboniferous era, while Caelifera first appears in the fossil record in the Triassic (Gorochov, 2001; Minards, 2011). Tree wētā belong to the older suborder Ensifera, which comprises two families, the Rhapidophoridae (Walker, 1871), or cave wētā, and the Anostostomatidae (Saussure, 1859), which is represented in New Zealand by five genera: the giant wētā *Deinacrida* (White, 1842), the tusked wētā *Anisoura* (Ander, 1932) and *Motuwētā* (Johns, 1997), the ground wētā *Hemiandrus* (Ander, 1938), and the tree wētā *Hemideina* (Walker, 1869).

Although their primary, pre-human habitats were lowland, mixed podocarp/broadleaf forests, and rocky mountain scree slopes (depending on the species of tree wētā), tree wētā are now commonly encountered in urban and suburban settings also, and thus may be the type of wētā that is most well recognised by the majority of people in New Zealand. There are seven recognised species of tree wētā , the Wellington tree wētā *H. crassidens* (Blanchard, 1851), the Hawke's Bay tree wētā *H. trewicki* (Morgan-Richards, 1995), the Canterbury tree wētā *H. femorata* (Hutton, 1898), the west coast bush wētā *H. broughi* (Buller, 1896), the Banks Peninsula tree wētā *H. ricta* (Hutton, 1898), the alpine scree wētā *H. maori* (Pictet & Saussure, 1891), and the Auckland tree *H. thoracica* (White, 1842) (Gibbs, 2001). Tree wētā can be found all across the New Zealand landmass, on the mainland and a number of lacustrine islands, but little is presently known about many of the most basic aspects of the ecology of these animals.

1.2 The Distribution of Tree Wētā in New Zealand

The seven species of tree wētā are distributed throughout New Zealand, typically in local allopatry, or parapatry, with other member of the same genus, but some species are distributed over a much wider area than others (Figure 1.1, accessed 21 July, 2013, from http://www.massey.ac.nz). The tree wētā are split into two monophyletic clades, based on phylogenetic analysis, one located on the North Island landmass, and the other located in the South Island (Morgan-Richards & Gibbs, 2001; Minards, 2011). *Hemideina crassidens, H. thoracica* and *H. trewicki* together comprise the northern group whilst *H. broughi, H. maori, H. femorata* and *H. ricta* form the southern group (Morgan-Richards & Gibbs, 2001; Minards, 2011). *Hemideina crassidens*, while considered a member of the North Island group, is the only species which occurs in both the North and South Islands.

Currently, the Auckland wētā *H. thoracica* is the most widely dispersed species of tree wētā in the North Island with a range of approximately 1800 km^2, and is mostly distributed throughout the upper half of the Island with a southern population near Levin (Morgan-Richards *et al*., 2001; Bulgarella *et al*., 2013). *Hemideina trewicki* is found in the Hawkes Bay area around Hastings, in a narrow zone of 40 km by 100 km, from the Kaweka Forest at the north of their range, down to the township of Porangahau on the southern coast of Hawkes Bay (Trewick & Morgan-Richards, 1995). This area overlaps the greater range of *H. thoracica* (Trewick & Morgan-Richards, 1995). In the Hawkes Bay area, *H. trewicki* and *H. thoracica* co-occur and appear to be fully sympatric, and may be frequently discovered occupying the same roosts (Trewick & Morgan-Richards, 1995). The Wellington tree wētā, *H. crassidens*, occupies Wellington, the Wairarapa area, and parts of the South Island from Kaihoka in the North, down the west coast to Milford Sound in the south (Trewick & Morgan-Richards, 1995; Field, 2001; Bulgarella *et al*., 2013) and is therefore the only wētā species which is present on both of the major landmasses of New Zealand. The potential distribution of *H. crassidens* appears to be limited by competitive interactions with *H. thoracica*, which is better adapted to warmer climates than *H. crassidens*, and gradual warming of the global climate has resulted in *H. crassidens* being pushed progressively south by range expansion of *H. thoracica* (Bulgarella *et al*., 2013). A population of the *H. crassidens* subspecies *H. crassidens* subsp. *crassicruris* exists on Stephens Island, located in the Cook Strait between the

North and South Islands (Moller, 1985). *Hemideina broughi* has a range that overlaps with *H. crassidens* in Nelson and the northern West Coast. *Hemideina ricta*, the Banks Peninsula tree wētā, is the most geographically restricted species of tree wētā and is known from only two locations on the Banks Peninsula: Okains Bay, and in tōtara (*Podocarpus totara*) logs near Purple Peak in South Canterbury. The Canterbury tree wētā *H. femorata* also occurs on Banks Peninsula, but its range extends over a greater area north and west of this (Townsend *et al*., 1997). Where both species are found in the same area, *H. ricta* and *H. femorata* are parapatrically divided by a combination of altitude and host-plant preference. The mountain stone wētā, *Hemideina maori*, has the southernmost distribution of all *Hemideina*, and inhabits scree slopes and rock outcrops in the alpine region of the South Island, frequently at altitudes between 1200-3600 m above sea level (Gibbs, 1998; Gwynne & Jamieson, 1998; Harris, 2003; Trewick *et al*., 2000; Leisnham & Jamieson, 2002).

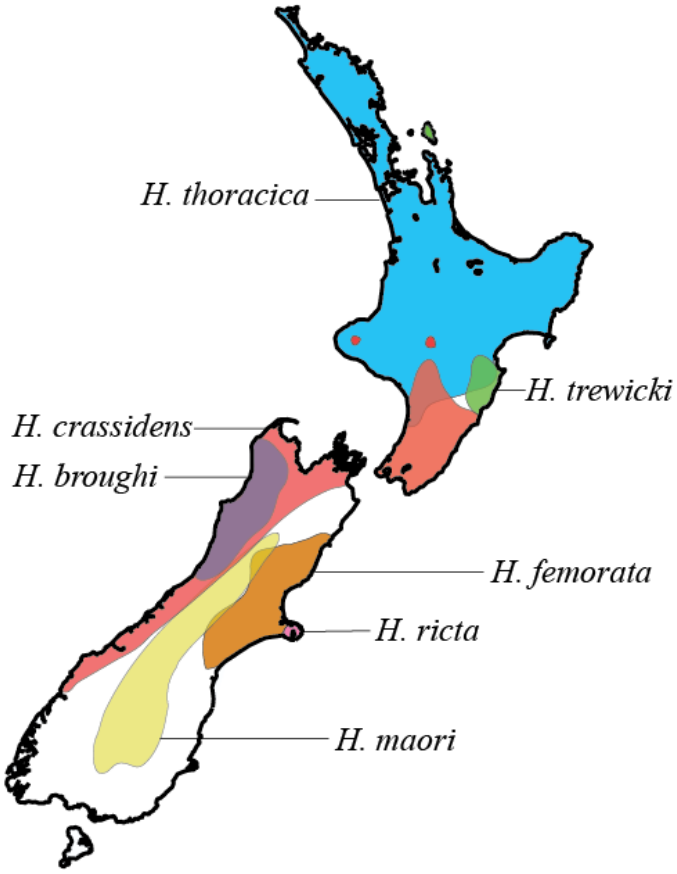

Figure 1.1. The current distribution of tree wētā species (accessed 21 July, 2013, from http://www.massey.ac.nz/~strewick/Root/Text%20files/treeweta.html).

1.3 Development, Morphology, and Sexual Dimorphism

All tree wētā are hemimetabolous and hatch from their eggs resembling scaled-down versions of the adult form, and then grow through a series of moults into sexually mature adults (Gibbs, 1998, 2001; Minards, 2011). Tree wētā are long lived insects, they take up to a year to grow to sexual maturity and have a total lifespan that can vary from 9 months to three years (Leisnham *et al*., 2003; Kelly, 2008; Minards, 2011; Wehi *et al*., 2013). All species in the genus *Hemideina* share distinct similarities in their morphology (Gibbs, 2001). Adults typically grow to a final length of between 40-70 mm (not including the antennae) with a smooth, shiny, capsule-shaped head, and a thorax that is divided into prothoracic, mesothoracic, and metathoracic regions covered by a saddle-like shield referred to as the pronotum (Field, 2001), and the abdomen possesses a series of ten abdominal tergites, which are softer and more pliant than the rest of the body (Gibbs, 2001).

With the exception of *H. broughi*, all *Hemideina* are sexually dimorphic (Figure 1.2). The sexually mature males are highly megalocephalic and possess an enlarged head that supports considerably larger mandibles than those possessed by the females, and may be up to 40% of the total body length of the male (Field, 2001; Gibbs, 2001; Morgan-Richards and Gibbs, 2001; Kelly, 2006a). The head of the adult male is not only substantially larger, but also darker, and more sclerotized than the heads of the females or juvenile instar males (Field, 2001). All female *Hemideina* mature in the 10^{th} instar, but males are trimorphic, and are capable of becoming sexually mature in the 8^{th}, 9^{th}, or 10^{th} instars. Because the megalocephalic development of the males mostly occurs in the final moulting, and is related to total body mass, the instar in which they achieve sexual maturity results in three possible morphotypes (Field & Deans, 2001; Kelly, 2008; Minards, 2011). Males that mature in the 8^{th} instar have the smallest mandibles, 9^{th} instar males are intermediate in mandible size, and 10^{th} instar maturing males have the largest mandibles (Stringer & Cary, 2001; Kelly, 2004; Kelly & Adams, 2010; Minard, 2011). Variation in the mandible size of female tree wētā is considerably smaller than that of the males, and early instar males closely resemble females in the appearance of their heads (Field, 2001). Other structural features that differentiate mature males from mature females are the presence of long curved sensory organs called ‘cerci’ on the posteriors of the males, and a

long, sharp and slightly recurved structure called an ‘ovipositor’ (a tapered tube for laying eggs) on the posterior of the females (Gibbs, 1998; Field, 2001; Minards, 2011).

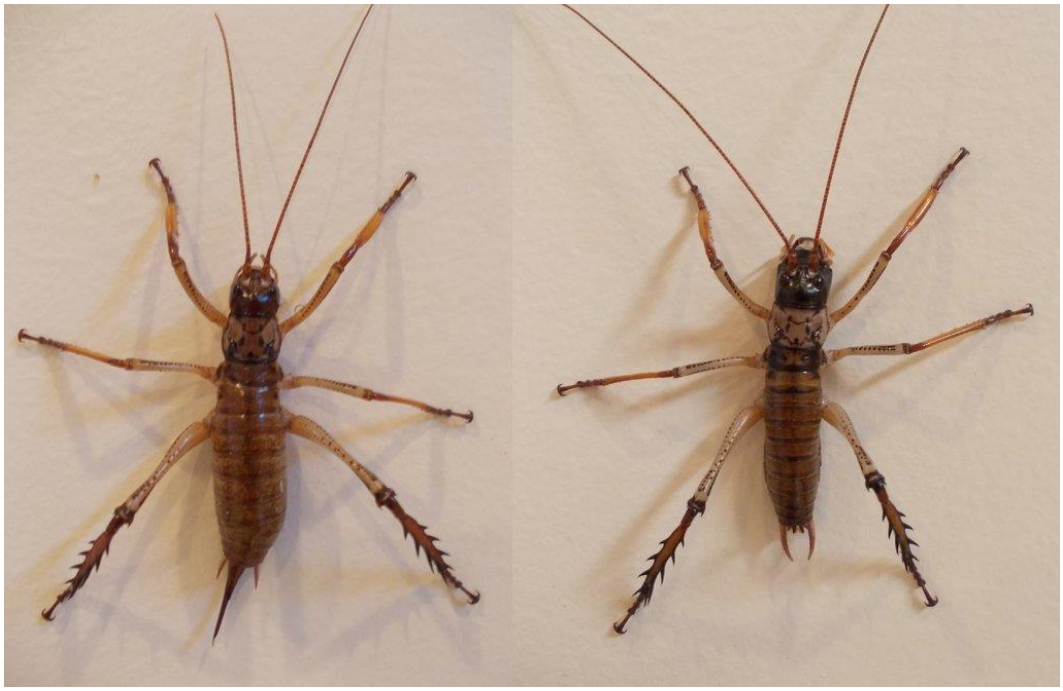

Figure 1.2. Dorsal view of female (left) and male (right) *H. thoracica* showing the enlarged abdomen and long ovipositor of the female, and the large, dark, sclerotized head, and elongated circi of the male. Photos by author (2013).

The tree wētā mating system is probably male dominance polygynandry (Kelly, 2006b), as described in Shuster and Wade (2003). Male tree wētā use their large mandibles to secure and defend tree holes, referred to as galleries, where they temporarily cohabitate with harems of female wētā (Field & Deans, 2001; Kelly 2006a, 2006b, 2006c; Minards, 2011). Wētā do not bore their own galleries, but will typically use wood holes that were originally excavated by wood boring insects such as cerambycid (*Ochrocydus hutoni*) or lepidoptera (*Aenetus virescens*) larvae (Field, 2001; Robinson, 2005). Residence in any gallery is transient, and when the male has successfully mated all of the females in a particular gallery, he will move on (Kelly, 2006b). This means that residence time is positively correlated with the size of the gallery, as larger galleries can accommodate more females.

1.4 Species Level Identification

The patterning and colouration of the pronotum shield (a structure formed from the fusion of the first three thoracic tergites) are considered the most reliable features for identifying *Hemideina* to the level of species (Field, 2001). The pronotum is distinctly coloured in most species of tree wētā, usually possessing a pattern of black or dark brown transverse markings in a field of a separate colour, and variation in this trait is found mostly in the thickness and the patterns of the dark markings (Field, 2001). *Hemideina crassidens*, *H. crassidens crassicruris*, *H. ricta*, and *H. broughi* have a dark background with darker markings, whereas *H. maori*, *H. femorata*, *H. thoracica*, and *H. trewicki* have a thin, dark markings on a pale pronotum (Figure 1.3). The darker markings on the pronota of each species indicate the fusion points between the thoracic tergites that formed the pronotum, named the scutum, the prescutum, and the scutellum. It is possible to key *Hemideina* to the level of species by using the background colour and transverse patterns of the pronotum alone (Appendix 1.1), as the field colour, and the shapes and thickness of the transverse bands, are relatively stable within each species.

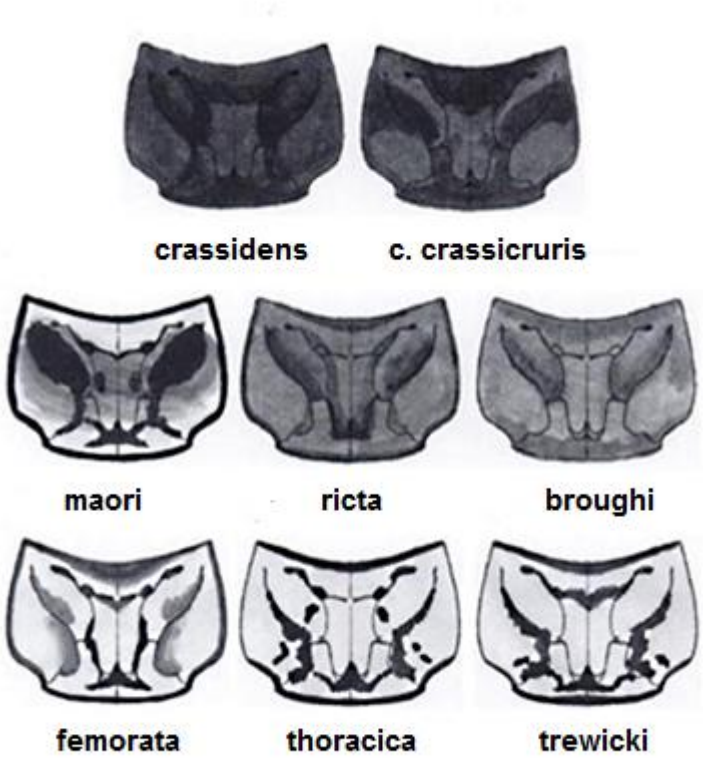

Figure 1.3. The pronotum of all known species in the genus *Hemideina*.

1.5 Threats to the Conservation of Tree Wētā

Many of the giant species of wētā are protected under the Seventh Schedule of the Wildlife Act of 1953, including *Deinacrida carinata*, *D. fallai*, *D. heteracantha*, *D. rugosa*, *D. parva*, and *D. tibiospina*, as is the Banks Peninsula tree weta *Hemideina ricta* (Sherley, 1998), but as of writing this, there are a total of 16 species of wētā listed as threatened in New Zealand (Appendix 1.2). Although they evolved alongside a variety of endemic predators, such as bats, birds, and reptiles, the addition of exotic, r-selected, mammalian predators has taken a heavy toll on wētā, and tree wētā numbers have declined to a fraction of their pre-human densities (Sherley, 1998; Ruscoe *et al*., 2012). Introduced predators now outnumber native predators, in terms of both species diversity and population density, and small introduced mammals, particularly ship rats (*Rattus rattus*, Linnaeus, 1758), ferrets (*Mustela furo*, Linnaeus, 1758), and hedgehogs (*Erinaceus europaeus*, Linnaeus, 1758), are now the main predators of tree wētā in New Zealand (Innes 1979; Jones & Sanders 2005; King & Murphy 2005; Ruscoe & Murphy 2005, Watts *et al*., 2008). It has been estimated that *Hemideina* are the most frequently consumed invertebrate for *Rattus* species in New Zealand (Ruscoe *et al*., 2012), and *Hemideina* wētā were found in the stomachs of 39 – 76% of trapped ship rats (Innes 2005). The number of *H. thoracica* that were captured in pitfall traps, in a fenced mainland ecological-reserve, increased 12-fold within two years after the removal of introduced mammals from the reserve, and the percentage of adult wētā caught in the traps increased by 30 % in that time (Watts *et al*., 2011), indicating that current tree wētā population densities may be less than 10 % of their pre-human numbers. It has even been observed that the normal behaviour of *H. crassidens* is affected by the presence of introduced predators, causing them to nest in smaller, less accessible galleries, higher above the ground, potentially altering their foraging behaviour (Rufaut, 1995). In addition to the recognised, threatened species, there are still many undescribed species of wētā for which there is insufficient data to assign a specific conservation status. For example, in 2010 there were an estimated 28 unnamed taxa of ground wētā, some of which are only known to science by a single specimen (Muckle & Chinn, 2010).

Tree wētā have suffered heavily from the presence of introduced predators, which many species of wētā are poorly equipped to defend against. On top of this,

there are the potential fitness-related impacts of their modified feeding environments, which now contain a large number of exotic plant species, as well as potential range shifts that are likely to occur in the near future from global climate change. To be better able to effectively conserve the remaining wētā, it should be a foremost object for restoration ecologists in New Zealand to gather as much information as possible about the population, functional, and nutritional ecology of these animals. More in-depth observations of tree wētā behaviour, will benefit our understanding of how tree wētā function in their ecosystems, which will enable future conservationists to develop more effective conservation strategies to curb the decline of these animals. This will not only benefit the wētā, but also the native vertebrates that feed on them, and thereby promote greater biodiversity in New Zealand.

1.6 Current Data on the Diet and Nutritional Ecology of Tree Wētā

1.6.1 Artificial Diet Studies Performed in Captivity

Many species of animals selectively forage based on the macronutrient content of available foods (Simpson & Raubenheimer, 2012). Protein and carbohydrates are among the nutrient groups that are most strongly regulated by herbivorous insects, and are thus expected to play a dominant role in ingestive behaviour (Simpson & Raubenheimer, 2000; Raubenheimer *et al*., 2009). Because of this many captive studies that have been performed with captive insects have measured their consumption of protein and carbohydrates. Most captive feeding studies performed on tree wētā have been performed using the Wellington tree wētā *H. crassidens*. Wehi *et al* (2013) used the geometric method to investigate whether or not *H. crassidens* are capable of balancing their consumption of the macronutrients protein and carbohydrates, and whether or not male and female tree wētā feed to establish different nutritional targets. They fed their wētā on artificial diets, with specific ratios of protein to carbohydrates (P:C), and then measured the consumption of the different diets over time, and found that *H. crassidens* feed to establish a carbohydrate rich diet (Wehi *et al*., 2013). Preferring a carbohydrate heavy diet in captivity may indicate that *H. crassidens* naturally consume more plant materials (carbohydrate heavy foods) in the wild

than they do other insects (protein rich foods). Whether this is the case could be explored though more examinations of their actual diet in the wild via faecal fragment analysis or isotope fractionation analysis.

It has been observed that tree wētā can grow to maturity on a purely herbivorous diet, which has contributed to a common notion, largely untested, that tree wētā are naturally herbivorous. Griffin *et al.* (2011) tested this assumption by offering captive *H. crassidens* a combination of leaves and fruit of *Coprosma robusta* in conjunction with fresh, freeze-killed *Wiseana* moths over two consecutive nights. They found that 87.5 % of the wētā ate some of the moths provided and that no wētā consumed only leaves, demonstrating that *H. crassidens* have the potential for omnivory in captivity. Griffin (2011) also measured the growth of two groups of juvenile tree wētā fed on two diets with variable quantities of protein. The first group was fed on the leaves of native plants (*Melicytus ramiflorus*, *Prumnopitys ferruginea*, *Coprosma robusta*, and *Coprosma repens*) and the other group was fed on the same foliage plus a soy-based protein supplement. They found that the protein supplemented group grew faster and accumulated more stored fat in the abdominal cavity, but this did not result in the production of a greater number of eggs, or more viable eggs, by the protein supplemented group (Griffin, 2011). The additional fat laid down by the high protein group may suggest that *H. crassidens* can benefit from some additional protein in their diet, as greater deposits of stored energy could mean that the wētā have to emerge less often from their tree cavities to forage, exposing themselves to predators less often. On the other hand, the fact that increased protein consumption did not increase the number or viability of eggs produced may mean that the optimal level of protein that *H. crassidens* need for peak performance is not very high, and can be achieved on a mostly vegetative diet, and that further protein consumption beyond this point does not result in any reproductive benefit. Whether or not *H. crassidens* may be more accurately described as an herbivore or an omnivore cannot be strongly supported either way by that experiment, but could be gauged by direct observations of their feeding behaviour in the wild.

Whether or not the Auckland tree wētā *H. thoracica* is capable of nutrient balancing, and if it selects for a specific ratio of protein to carbohydrates when it forages, has not been determined, neither has it been determined how efficiently they digest and metabolise protein and carbohydrates.

1.6.2 Dietary Studies Performed on Wild Tree Wētā

Although the nutritional ecology of tree wētā is still relatively unexplored, studies of *Hemideina* in the wild have been gaining momentum in recent years. Two studies have been performed on the diet of the Auckland tree wētā *H. thoracica*, a radio isotope fractionation analysis (Wehi & Hicks, 2010), and a faecal fragment analysis (Dewhurst, 2012). Wehi & Hicks (2010) used isotope fractionation to investigate the diets and trophic interactions of *H. thoracica*. They captured 12 *H. thoracica* from the wild, froze five, and then fed each of the other seven a different native plant for four days, and collected all the faeces (referred to as 'frass') that they produced in that time, before freezing them as well. After grinding a variety of tissues from the frozen wētā they performed isotope fractionation analysis on the collected frass and the prepared tissues. Comparing the isotopes in the plants fed to the captive *H. thoracica* to the isotope ratios in the frass provided variable results, and it was determined that frass isotope analysis was of limited usefulness in determining the trophic level of this animal (Wehi & Hicks, 2010). There was no significant difference in isotopic values between adults and juveniles, indicating that the diet of the adults does not differ from that of the juvenile wētā, and there was also no significant difference between the captive *H. thoracica*, and those that were frozen immediately after retrieval from the wild, suggesting that *H. thoracica* is primarily herbivorous in the wild (Wehi & Hicks, 2010).

Dewhurst (2012) performed a fragment analysis on the frass of wild *H. thoracica* captured from the western foothills of the Tararuas. They compared the composition of the plant fragments in the frass to the composition of the vegetation surrounding the locations where the wētā were captured, and identified the fragments of 28 species of plants, with an average of 2.65 ± 0.26 plant cuticles per frass pellet, there was no significant difference in the number of plant species consumed by males and females (Dewhurst, 2012). Only 6 of the 31 wētā had exclusively eaten plants from within the immediate quadrate, and many wētā did not consume the plants that they were most likely to encounter after leaving their gallery, indicating that *H. thoracica* frequently travel more than 3.13 m from their gallery, and forage selectively.

Dewhurst (2012) performed a captive feeding trial using a mixed group of *H. crassidens* and *H. thoracica* using leaves from eight different native plants,

with the purpose of determining whether tree wētā prefer leaves with high nitrogen content. The plants most preferred by the wētā were *Coraria arboria* and *Carpodetus serratus*, which had the highest N concentrations of all plants in the study (> 2%), and the plants with the lowest N assimilation were the least preferred (*Fuchsia excorticata* and *Griselinia littoralis*) (Dewhurst, 2012). However, nitrogen rankings did not successfully predict the preference of any other plants in the study, indicating that there must be other factors that determine plant palatability to foraging wētā.

Evidence is accumulating that the concentration of lipids and oil glands in the leaves is another factor that tree wētā use to select between plant species. Multiple studies have been performed on the diet of the mountain stone wētā *H. maori*, all of which involved identifying cuticles in wētā faeces (referred to as 'frass') collected from the field (Little, 1980; Lodge, 2000; Joyce, 2002; Wilson, 2004). They found that the lipid rich plant species *Anisotome imbricata*, *Abrotonella inconspicua*, *Celmisia viscosa*, *Celmisia brevifolia*, *Helichrysum selago*, *Kelleria villosa*, *Leptospermum scorparum*, *Poa colensoi*, *Podocarpus nivalis*, and *Raoulia hectori* were consumed more often than other plants which were more abundant in the immediate vicinities, and this suggests that lipid content is an important factor in the foraging decisions of *H. maori*.

Consumption of other insects also appears to be common among *H. maori*. Little (1980) found that invertebrate fragments were present in 80 % of all wild frass pellets produced by *H. maori* at Jacks Pass (near Hanmer in Canterbury), and constituted 5 % of all identifiable faecal fragments, and Lodge (2000) and Wilson (2004) both found that invertebrate fragments accounted for 10% of all identifiable fragments recovered from the frass of wild *H. maori* from the Rock and Pillar range (Otago). Tree wētā may regularly exploit other invertebrates as food, and the results of all of these studies indicate that *H. maori* are naturally omnivorous.

Whether or not the Auckland tree wētā *H. thoracica* forages selectively, and preferentially selects for lipid rich plants, has not been determined, nor has it been determined if they are better described as herbivores or omnivorous.

1.7 Thesis Outline: Aims and Purpose of this Study

Understanding an animal's nutritional needs is fundamental to understanding that animal's functional role in its natural habitat, and predicting how it might function in a new or modified habitat. I aim to improve the current level of understanding surrounding the ecology of tree wētā by exploring the nutritional aspect of the functional ecology of the Auckland tree wētā *Hemideina thoracica*. To achieve this, I conducted three studies that were designed to determine what *H. thoracica* eat in their natural environment, whether they forage to achieve a specific nutritional target, and whether it is likely that *H. thoracica* may act as seed dispersers for plants in the wild.

1.7.1 Chapter Two

I present the results of a faecal fragment analysis that I performed on the frass of wild *H. thoracica* from the Waingaro Forest Reserve. The purpose of this was to determine what *H. thoracica* eat in the wild, whether they are better described as herbivores, or omnivores, and if they preferentially select lipid-rich leaves. I also compared the composition of the frass to the composition of the vegetation communities in the areas where the wētā were captured, in order to determine whether or not *H. thoracica* feed randomly on the plants that are available, or if they display a high degree of selectivity when foraging.

1.7.2 Chapter Three

I present the results of a captive feeding trial that used a combination of the geometric and gravimetric methods to determine whether *H. thoracica* can regulate their intake of protein and carbohydrates (nutrient balancing), whether they feed to achieve a specific ratio of protein to carbohydrates, and how efficiently they digest and utilise these two macronutrients.

1.7.3 Chapter Four

I present the results of a trial that investigated whether *H. thoracica* feed in a manner that may facilitate the dispersal of seeds in the wild. This involved feeding a group of 40 captive *H. thoracica* the berries of three native plants and recording which structures of the fruit were consumed, whether or not the seeds of the fruit were ingested, and whether or not any ingested seeds passed intact through the alimentary canal of the wētā.

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2 Chapter 2: An Analysis of the Diet of the Auckland Tree wētā *Hemideina thoracica*.

2.1 Introduction

The Auckland tree wētā (*Hemideina thoracica*, White, 1842, Orthoptera, Anostostomatidae) is a large, flightless, terrestrial insect that is endemic to New Zealand. There are currently seven recognised species of tree wētā, all of which belong to one genus, and which are distributed throughout the North and South Islands of New Zealand. *Hemideina thoracica* are the most widely distributed species of tree wētā in the North Island, and they are common throughout the upper two-thirds of the landmass of that island, but as they are cryptic, nocturnal animals, it is difficult to observe the foraging behaviour of *H. thoracica* in the wild. Because of this, relatively little is known about their natural diet, including the species of plants that they feed on, whether they are herbivores or omnivores, and whether or not they forage selectively (Wehi & Hicks, 2010; Griffin, 2011; Dewhurst, 2012).

Tree wētā are an important food source for many of the endemic vertebrates of New Zealand, including bats, kiwi, parrots, owls, and tuatara, among others, but neither the trophic position, nor the structural importance, of tree wētā in the food webs of New Zealand's forest ecosystems have been fully determined. Since human arrival in New Zealand, tree wētā numbers have been severely reduced by predation by introduced, high density, mammalian predators (Sherley, 1998; Watts *et al*., 2008, 2011; Ruscoe *et al*., 2012), particularly ship rats (*Rattus rattus*, Linnaeus, 1758), ferrets (*Mustela furo*, Linnaeus, 1758), and hedgehogs (*Erinaceus europaeus*, Linnaeus, 1758) (Innes, 2005; Jones & Sanders 2005; King & Murphy, 2005; Ruscoe & Murphy, 2005). To be able to conserve any species, scientists need to understand its basic ecological requirements, such as what its diet is composed of, and why it eats that diet. By increasing our understanding of tree wētā ecology, New Zealand conservationists may be able to develop conservation strategies that more effectively curb the decline of these animals, which would benefit both the wētā, and the native vertebrates that feed on them.

It has been observed that tree wētā can grow to maturity on a purely herbivorous diet, which has contributed to a common notion, largely untested, that tree wētā are naturally herbivorous in the wild (Griffin *et al*., 2011). In recent years, two studies have been performed on the diet of *H. thoracica* in the wild, a radio isotope fractionation analysis (Wehi & Hicks, 2010), and a faecal fragment analysis (Dewhurst, 2012). Wehi & Hicks (2010) used isotope fractionation to investigate the diet and trophic relationships of *H. thoracica* captured from three urban forests in the Hamilton Ecological District. They found that whole-body values of $\delta^{15}N$ and $\delta^{13}C$ did not differ significantly between *H. thoracica* retrieved from the wild and then immediately frozen, and *H. thoracica* fed on native plants in captivity, supporting the notion that this species is primarily herbivorous in the wild. Dewhurst (2012) performed a fragment analysis on the frass of wild *H. thoracica* captured from the western foothills of the Tararuas, and identified the fragments of 28 species of plants, with an average of 2.65 ± 0.26 plant cuticles per frass pellet (Dewhurst, 2012). While that study also supports the theory that leaves are the biggest component of the diet of *H. thoracica* in the wild, Dewhurst (2012) also mentioned that invertebrate fragments were present in the frass, but did not quantify the frequency or abundance of invertebrate fragments relative to plant fragments. Therefore, it is possible that *H. thoracica* are actually naturally omnivorous, rather than herbivorous, and this could be determined by quantifying the frequency of occurrence, and the overall density of invertebrate fragments in the frass of wild *H. thoracica*, relative to plant fragments.

Determining the factors that influence an animals diet can be complicated, as there are many factors that could be involved in any trophic interaction, but how and why a species consumes the items that make up its diet are questions that need to be asked and answered before the ecology of the animal can be understood. Dewhurst (2012) performed a captive feeding trial to determine whether tree wētā preferentially select leaves that have a high nitrogen content. *Coraria arboria* and *Carpodetus serratus*, which had the highest N concentrations of all the tested plants (> 2%), were the most preferred species, but nitrogen rankings did not successfully predict the relative preference of many other plants in their study, indicating that there are other nutrients that determine the palatability of different leaves to foraging tree wētā. Faecal fragment analyses that have been performed on the closely-related mountain stone wētā *H. maori* have indicated that *H. maori* may preferentially consume plants that have high

concentrations of lipids and oil glands in their leaves (Little, 1980; Lodge, 2000; Joyce, 2002; Wilson, 2004; Wilson & Jamieson, 2005). These studies revealed that plant species with high concentrations of lipids and oil glands in their leaves, were often eaten more frequently, and in greater quantity, than other plants which were more abundant in the immediate vicinity. Whether other species of tree wētā, such as *H. thoracica*, preferentially select lipid rich plant leaves has not been investigated.

Herbivorous insects often have important ecosystem functions (Patrick, 1994) and performing more studies on the functional and nutritional ecology of cryptic foragers like *H. thoracica*, in the wild, will improve our understanding of how such animals operate within their ecosystems, and thereby improve our understanding of how those ecosystems function. I used the faecal fragment method of dietary analysis to determine what a population of wild *H. thoracica* had been eating in a mixed podocarp/broadleaf forest, in the Raglan Ecological District of the Waikato Region of New Zealand. The fragment analysis method is considered one of the best and most accurate methods for determining the diets of animals that are difficult to observe feeding (Wilson, 2004), and the purpose of this study was to answer the following questions;

- What do *H. thoracica* eat in the wild?
- Are *H. thoracica* better described as herbivores, or omnivores?
- Do *H. thoracica* forage randomly, or selectively?
- Do *H. thoracica* preferentially select the leaves of plants that have high concentrations of lipids and oils?

I captured 45 *H. thoracica* from the wild, collected the faecal pellets (referred to as 'frass') that they subsequently produced in captivity, and identified the undigested food fragments contained in the frass in order to determine what they had recently consumed in a natural setting. The faecal fragment data was compared against the vegetation composition of the forest, which I recorded via the reconnaissance plot sampling technique, and a solvent extraction was performed on the leaves of a variety of plant species that were positively identified in the frass. This combination of analyses enabled me to determine what *H. thoracica* eat in the wild, whether or not they forage selectively, whether they are better described as herbivores or omnivores, and if they might preferentially consume the leaves of plants that have a high lipid concentration.

2.2 Materials and Methods

2.2.1 The Study Site: Vegetation Sampling and Collecting Wētā

Mixed podocarp/broadleaf forests were common in the lowland and montane areas of the North Island of New Zealand prior to human arrival, and still represent a significant, natural habitat for many endemic animals, and as such, represent ideal locations for studying the trophic aspects of the functional ecology of native animals in a natural setting. *Hemideina thoracica* were collected on a privately owned section of mixed podocarp/broadleaf forest that forms part of the Northern edge of the Waingaro Forest Reserve, in the Waingaro region of the Raglan Ecological District (Figure 2.1). The property forms a small catchment, located on a hill slope, and is drained by a first order stream that bisects the property down the middle and feeds into another first-order stream that runs roughly parallel to the base of the hill-slope along a flat plateau. The site faces west, and the slope has a moderate to steep aspect. The elevation increases from a mean elevation of 47.1 m above sea level at the plateau (based on ten GPS readings taken across the width of the property), up to a mean elevation of 127.5 m above sea level at the hillcrest. The property is roughly divided into six topographical zones; the terrace, the lower hillslope, the mid hillslope, the upper hillslope, the basin, and the hillcrest. Drainage and exposure both increase from the terrace (the most poorly drained and the lowest amount of exposure) up to the hillcrest (the most well-drained and the highest level of exposure) and the floral community changes along this gradient between zones, in response to the changes in these two variables.

Vegetation sampling was carried out from mid-February through to March of 2013. The reconnaissance (recce) plot sampling technique (Hurst & Allen, 2007) was used to determine the relative ground cover of all of the plant species in each of the topographical zones on the property. The recce forest sampling technique records the overall area of ground covered (%), at each of six vertical tiers (m), for every species of plant in the plot. Ten 12 m^2 recce plots were recorded in each zone, and the data derived from these plots was used to determine the mean ground cover (%) of each recorded species, at each tier, in each zone (Appendix 2.1). After recording the vegetation composition of the site, I went from plot to plot extracting and collecting *H. thoracica* from dead branches, fallen logs, and any privet (*Ligustrum sinense*), that had likely-looking cavities. A

total of 45 *H. thoracica* were captured from the terrace, the mid hillslope, and the upper hillslope zones, in an approximately 1:1 male to female ratio, and then returned to the animal house facilities at the University of Waikato to collect their frass.

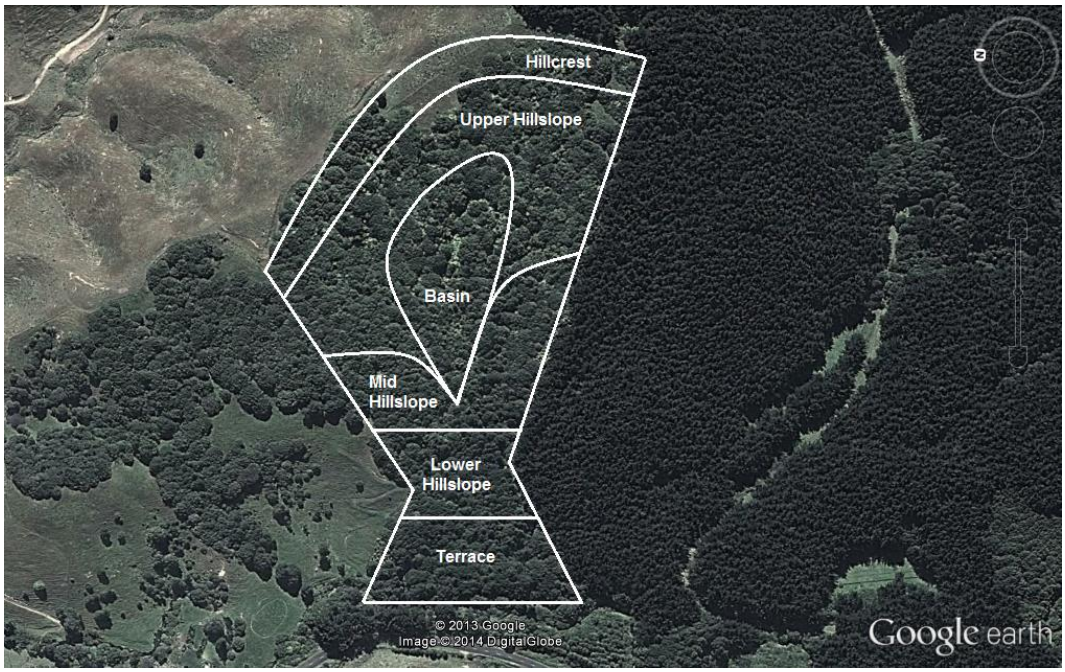

Figure 2.1. A satellite photograph of the study site, which was located on the northern edge of the Waingaro Forest Reserve, in the Raglan Ecological District of the Waikato Region of the North Island of New Zealand, located at 37°40'25.74"S and 174°58'21.33"E, and with the six basic topographical zones marked in white (Google Earth, 2013).

2.2.2 Collecting and Processing Wētā Frass

For the first four days after capture, all of the frass produced by the captive wētā was collected and placed in labelled 5 ml tubes, until all of the wētā had ceased producing frass. In total, the wētā produced 107 frass pellets, which were stored at -20ºC until they could be processed. Each pellet was processed in the following manner. The frass was placed in a mortar with 5 ml of distilled water, teased apart in to small pieces with a metal probe, and then gently ground into a solution with a pestle. The solution was poured through a triangular paper coffee-filter, leaving a layer of fine, faecal material on the filter, which was transferred onto one or more microscope slides using a flat headed probe (large pellets had to be made into multiple slides to prevent crowding of fragments). One or two droplets of distilled water was added to each slide with a Pasteur pipette, and another flathead

probe was used to ‘dab’ the material to cause it to disperse evenly across the slide. After the water had been evaporated using a hot-plate, the fragments were stained for viewing using a basic fuchsin gel, and a cover slip was applied on top. All of the slides were labelled with the sex of the wētā, as well as the plot and location where the wētā had been collected.

2.2.3 Identifying and Recording Faecal Fragments

To identify the microscopic food fragments that had been extracted from the frass, I built a database of photographs of the cuticles, stomata, trichomes, oil glands, and any other outstanding features of the leaves, and, where available, flowers, fruits, and seeds, of the most prolific plant species at the study site. This was done by using the recce plot data to compile a list of all of the plants that were recorded at the site, separating the wētā into groups of three, starving them for 48 hours to empty their guts, and then feeding each group on a different plant from the list. The frass that each group produced was processed and made in to microscope slides in the same manner as the wild frass, and then photographed at 200 and 400 times magnification using a Leica DMRE light microscope. The final library was composed of around 1500 individual photographs, documenting multiple cell-level structures of 51 of the most common indigenous and exotic plant species present at the site. This resource will continue to be expanded upon, and will eventually be made available for use by other researchers.

The faecal fragments that had been extracted from the wild frass were identified and counted at 400 × magnification, using a Leica DMRE light microscope to determine the relative abundance (%) of fragments from different species of plants. In order to save time, if 50 fragments of a particular type were counted in a single slide, those fragments would cease being counted in that slide, and extrapolation was used to estimate the total count. The relative abundance method was used to record faecal fragments, rather than the present/absent technique, because the present/absent technique often produces a false image of the relative ranking of items in the diet of an animal. For example, if one plant occurred in 80 % of all frass pellets, but only constituted 5 % of all fragments, and another plant occurred in 70 % of all pellets, but made up 50 % of all fragments, the plant that occurred in more pellets would still be recorded as the most preferred item under the present/absent method.

2.2.4 Comparing Leaf Availability against Fragment Composition

An established method for identifying the diet of herbivorous generalists is to compare the counts of faecal fragments belonging to different plant species against the relative ground cover of those plants (Wilson, 2004; Bekhuis *et al*., 2008; Dewhurst, 2012). When the frass produced by the captive wētā had been processed and analysed, the picture of their diet suggested that the *H. thoracica* at the study site had been foraging on the forest floor (for reasons which are discussed in better detail later). If tree wētā forage on the forest floor, then as far as foraging tree wētā are concerned, the area of ground covered by any tree is approximately equal to its leaf-fall area. To compare the fragment composition of the frass against the relative availability of different leaves, the average leaf-fall area of each species were determined using the data from the recce plots.

The mean ground cover was determined for each plant species, at each tier, and the highest value was used as the overall ground cover for each species. For example, in the mid hillslope zone, *Beilschmiedia tawa* had mean cover values of 7.5 %, 22.5 %, 17.5 %, 11%, 2.5 %, and 2.6 % at tiers one, two, three, four, five, and six, but for the purpose of comparison, *B. tawa* coverage at the mid hillslope was simply recorded as 22.5 % (the highest value). Recording the vegetation coverage in this manner converted the reccce plot data into an approximate representation of the leaf-fall area of each species. Figure 2.2 demonstrates the principle.

With the recce method, the overall cover for the different species typically combines to greater than 100 %, as multiple species often overlap the same area of ground. To be comparable to the fragment composition of the frass, the ground cover data needed to be adjusted to equal 100 %, and so the mean ground cover for each species was adjusted into a percent of the total cover. This enabled me to determine ‘expected fragment counts’ for each plant species, to compare against the actual observed counts. If *H. thoracica* forage non-selectively, then their consumption of any species of plant should be approximately equal to the availability of that species, based on its adjusted ground cover. For example, if 10,000 fragments were identified in the frass from the terrace, and *P. taxifolia* had an adjusted ground cover of 30 %, the expected fragment count for *P. taxifolia* at the terrace would be 3,000, but if the observed count were much lower than this, it could indicate that *H. thoracica* reject *P. taxifolia* as a food source.

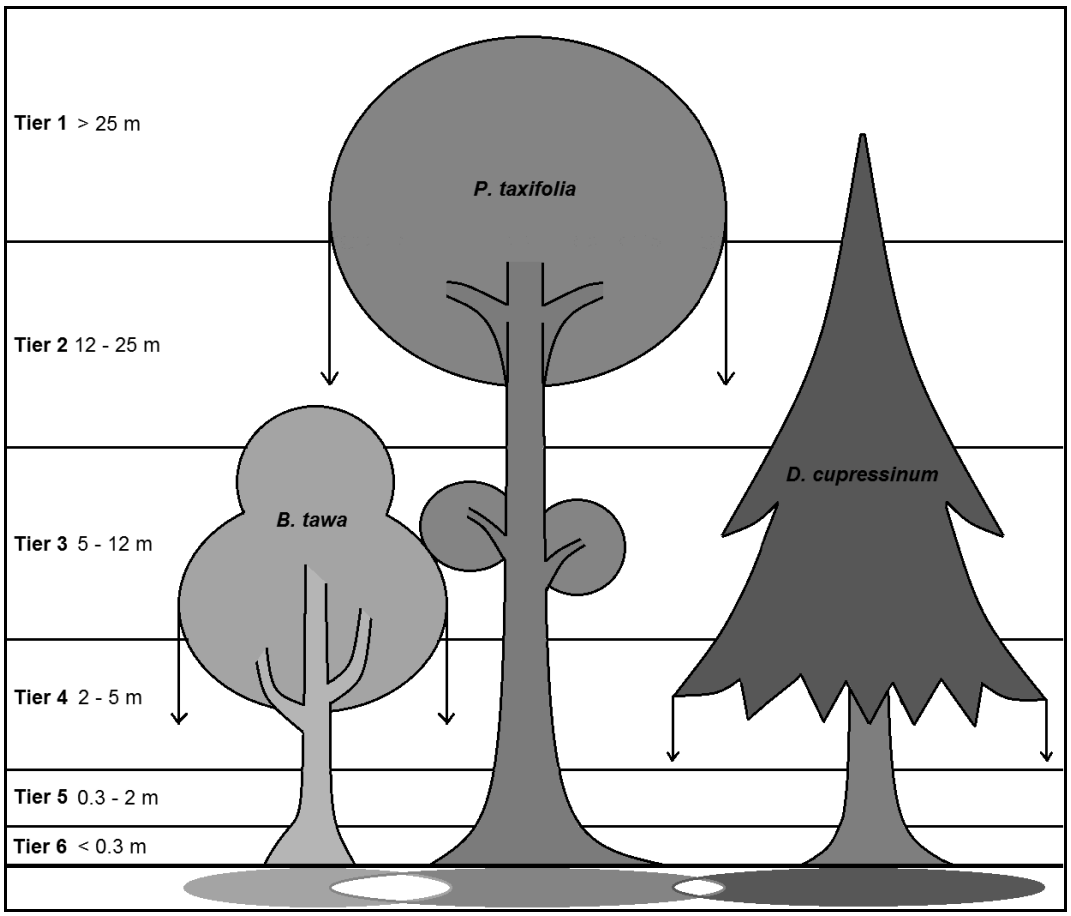

Figure 2.2. A hypothetical recce plot that shows how most tree species have some coverage in multiple tiers of the forest column. However, recording only the tier with the highest coverage, for each species, creates an approximation of the leaf-fall area for each tree (represented by the downwards facing arrows and corresponding coloured ovals), and thus the relative availability of different leaves to animals foraging on the forest floor. Image by Author (2013).

2.2.5 Solvent Extraction

A solvent extraction as performed to separate the lipids and oils from tissue samples of the leaves of eight plant species that were highly represented in the wild wētā frass (*Kunzia ericoides*, *Pennantia corymbosa*, *Prumnopitys taxifolia*, *Podocarpus totara*, *Melicytus micranthus*, *Melicytus ramiflorus*, *Coprosma rotundifolia*, and *Carpodetus serratus*), and eight species that were common at the site, but which were not consumed by the wētā (*Cyathea dealbata*, *Dacrycarpus cupressinum*, *Dicksonia fibrosa*, *Geniostoma ligustrifolium*, *Ligustrum sinense*, *Myrsine australis*, *Microstegium vimineum*, and *Selaginella*) for the purpose of comparison. Hexane was used as the solvent, as it produces higher oil yields than other solvents, such as ethanol (Ferreira-Diaz *et al*., 2003). To perform the extraction for each species, 1 g of leaf material was weight out and thoroughly

macerated with a mortar and pestle, and then transferred into a labelled falcon tube with 10 ml of water and 5 ml of hexane. The tubes were placed in an ultracentrifuge set on high speed for ten minutes to separate out the hexane phase, which contains the lipids and oils that were present in the original sample. The hexane phase was removed from each sample with a Pasteur pipette, and then transferred into labelled, pre-weighed, 10 ml glass tubes. The samples were placed under a fume hood, and streams of compressed air were directed into the samples to volatise the hexane, leaving behind only the oils and lipids. The tubes were then reweighed, and the concentration of lipids and oils was calculated for each.

2.2.6 Statistical Analysis

Microsoft Excel and Statistica 11.0 were used to analyse the data. One way ANOVA was employed to compare the fragments produced by male and female *H. thoracica*, to determine if there were any significant differences in the composition of the diets consumed by each sex. The number of plant species present, the species composition of those fragments, and the density of fruit, seed, and invertebrate fragments in the frass of male and female *H. thoracica* were analysed for each sample zone. No significant differences were detected, so for all further analyses male and female wētā were pooled together.

The contribution of each item to the total number of fragments identified in each sampling zone was calculated, and the overall composition of the diet in each area was explored graphically. One way chi-squared tests were used to compare expected vs. observed fragment counts for each recorded plant species, in each sample zone. Plant species that made up < 5 % of all ground cover were excluded from this analysis, as there were many such species in any area, which would have resulted in excessive degrees of freedom if included.

The concentration of invertebrate fragments, and fragments of fruits and seeds, appeared to differ between zones. One way ANOVA was used to determine if these differences were significant ($p < 0.05$), and Tukey's HSD post-hoc comparison was performed to determine which areas differed significantly from the others. To test whether there was a significant difference in the concentration of lipids and oils in the leaves of plants that the wētā consumed, compared to plants that were not consumed, the solvent extraction data was also analysed using one way ANOVA, and subjected to Tukey's HSD post-hoc comparison.

2.3 Results

2.3.1 Overview of the Plant Community of the Study Site

The most abundant species in the canopy of this zone was *P. taxifolia*, with an average coverage of 55 %, based on the ten recce plots recorded in this area (Appendix 2.1 A), followed by *D. dacrydioides* (17.5 %), and *P. totara* (12.5 %). The understory was dominated by *L. sinense*, which occurred in 100 % of the plots sampled in this area, and scored an average ground cover of 65 %, followed by *C. rotundifolia* (23.0 %), *Melicytus* (12.5), *C. dealbata* (11.5 %), *P. corymbosa* (5.5 %), and *Coprosma robusta* (5%), with a handful of other species making up less than 5 % each. The shrub layer was primarily composed of saplings of *L sinense* (40 %), *C. rotundifolia* (12.1 %), *R. sapida* (7.2 %), *Melicytus* (6.5 %), *P. corymbosa* (5.5 %), and young *C. dealbata* (5 %), with saplings of all other species making up less than 5 % each. The groundcover was predominantly leaf litter and clubmosses (*Selaginella*), with bamboo grass (*M. vimineum*) occurring around the banks of the Kahuhuru stream, which flows adjacent to this part of the section. 18 tree wētā were captured here, including nine males and nine females. 13 of these wētā were extracted from wood holes bored into the stems of live *L. sinense* by puriri moth larvae *(Aenetus virescens*), five were extracted from one large rot-hole in the base of a matai, and one was extracted from a dead *C. rotundifolia*. One male and one female produced no frass, so neither of these two are included in any further discussion.

In this zone, the most prolific tree in the canopy was *B. tawa*, with an average coverage of 22.5 %, followed by *P. taxifolia* (20 %), *P. totara* (15 %), *Dacrycarpus dacrydioides* (10 %), and *D. cupressinum* (7.5 %) (Appendix 2.1 B). The understory was dominated by the tree ferns *C. dealbata*, *Cyathea medullaris*, and *D. fibrosa* (47.5 %, 10 %, and 12.5 % coverage each respectively), followed by a variety of angiosperms, including *B. tawa* (11 %), *K. ericoides* (10 %), *Melicytu*s (8 %), *L. sinense* (7.5 %), *C. serratus* and *G. ligustrifolium* (5 % each). The shrub layer vegetation was also abundant with ferns, with young *C. dealbata* being the most common (35.5 %) and assorted *Blechnum* species making up another 20 %. These were associated with numerous angiosperm saplings, the most prolific of which were *Melicytus* (13.5 %), *L. sinense* (13 %), various *Coprosma* species (12.7 %), and *P. corymbosa* (6 %). Epiphytes were common, particularly *Microsorum* ferns (10.5 %) and climbing rata *Metrosideros diffusa*

(7.6 %). Most of the ground cover was composed of leaf litter and fallen branches. 13 tree wētā were captured here, including five males and eight females. Nine of these were extracted from wood holes in the trunks and dead branches of *K. ericoides*, two were extracted from wood holes in live *L. sinense*, and two were extracted from dead *P. totara*.

The most prolific canopy tree was *P. totara* (51.5 %), followed by *B. tawa* and *K. ericoides* (25 % each) (Appendix 2.1 C). The sub-canopy vegetation was dominated by *C. dealbata*, *K. ericoides*, and *P. totara* (20 %) each, followed by *Melicytus* (13.5 %), *Litsea calicaris* (8.5 %), *C. rotundifolia* and *G. ligustrifolium* (7.5 % each), and *C. serratus* (5 %). The shrub layer vegetation was dominated by young *C. dealbata* (25 %), as well as saplings of *Melicytus* (14 %), *K. excelsa* (8.6 %), *G. ligustrifolium* (8.5 %), *M. australis* (6.5 %), *C. rotundifolia* and *Pseudopanax crassifolius* (5.5 % each), and the ground cover was mostly *Selaginella* (20 %) and *M. vimineum* (13 %), plus leaf litter. 14 tree wētā were captured here, including seven males and seven females. 12 of these wētā were extracted from wood holes in dead branches of *K. ericoides* and the other two were extracted from a hole in a dead branch on a totara.

2.3.2 Using the Cuticle Library as an Identification Tool

The cuticle fragment library was effective for accurately identifying the fragments present in the frass of the wild *H. thoracica*. The morphological features that were most useful for successfully identifying fragments to the level of species were the size, shape, and arrangement of the stomata (Figure 2.3), the size, shape and arrangement of the epidermal cells (Figure 2.4), and the length and shape of the leaf hairs/trichomes (Figure 2.5), all of which displayed a high level of diversity. Some plants displayed similar characteristics in one, or even two, of these features, but no plants were alike for all three. Invertebrate fragments were also present in the frass, but were visibly distinct from the plant fragments. Invertebrate fragments typically included bits of exocuticle and endocuticle from the exoskeletons of various insects, as well as antennal fragments, pieces of compound eyes, tarsal claws, and leg joints and segments (Figure 2.6).

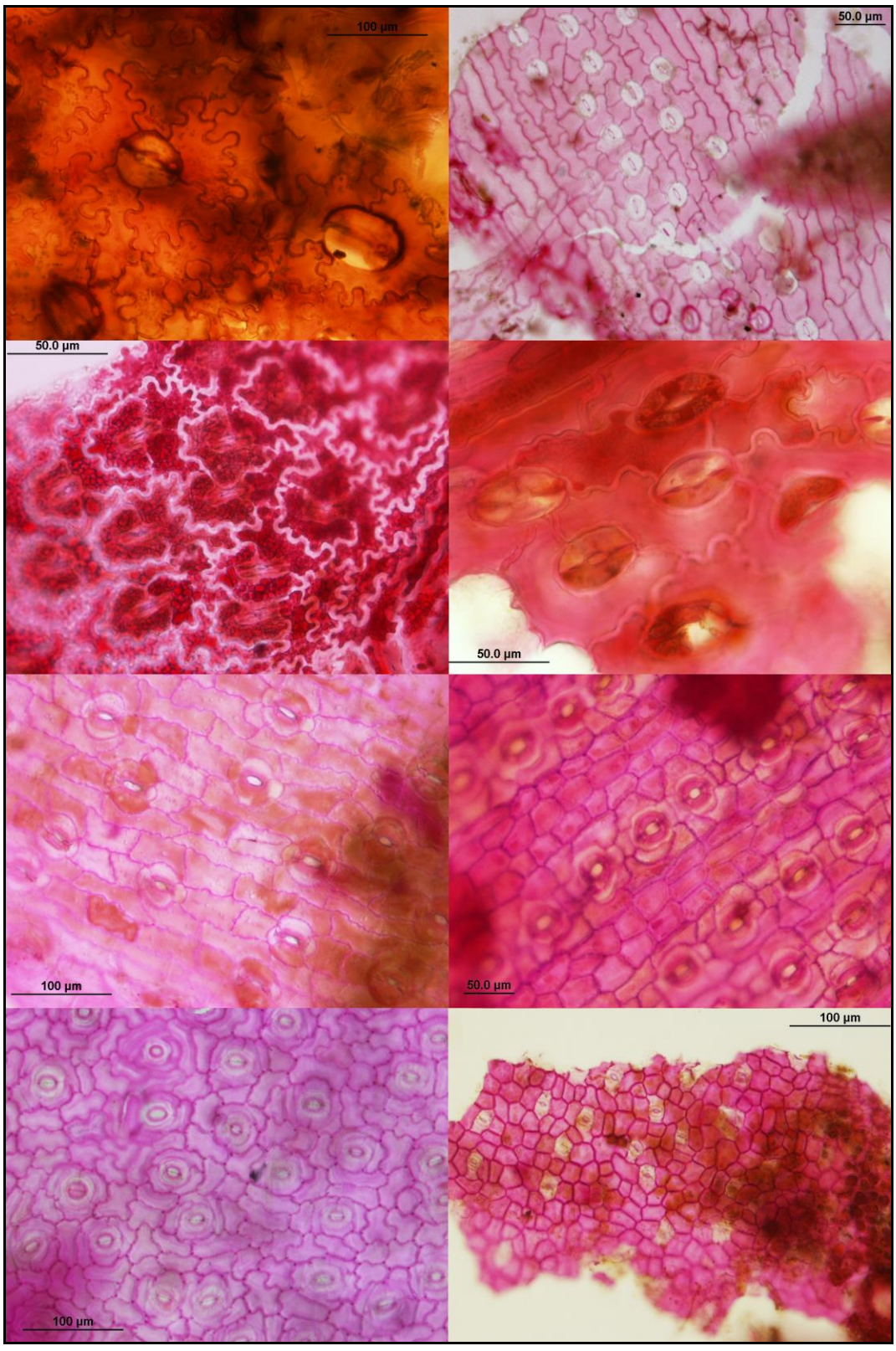

Figure 2.3. A selection of images from the plant cuticle database, demonstrating the morphological variety that occurs in the size, shape, and arrangement of the leaf stomata between species. First row, *Blechnum colensoi* (left) and *Selaginella* (right). Second row, *Cyathea dealbata* (left) and *Dicksonia squarrosa* (right). Third row, *Prumnopitys taxifolia* (left) and *Podocarpus totara* (right). Fourth row, *Pseudopanax crassi*folius (left) and *Kunzia ericoides* (right). The red/purple hue of the fragments is due to the fuchsin dye that was used to stain the samples. All photographs by the author (2013).

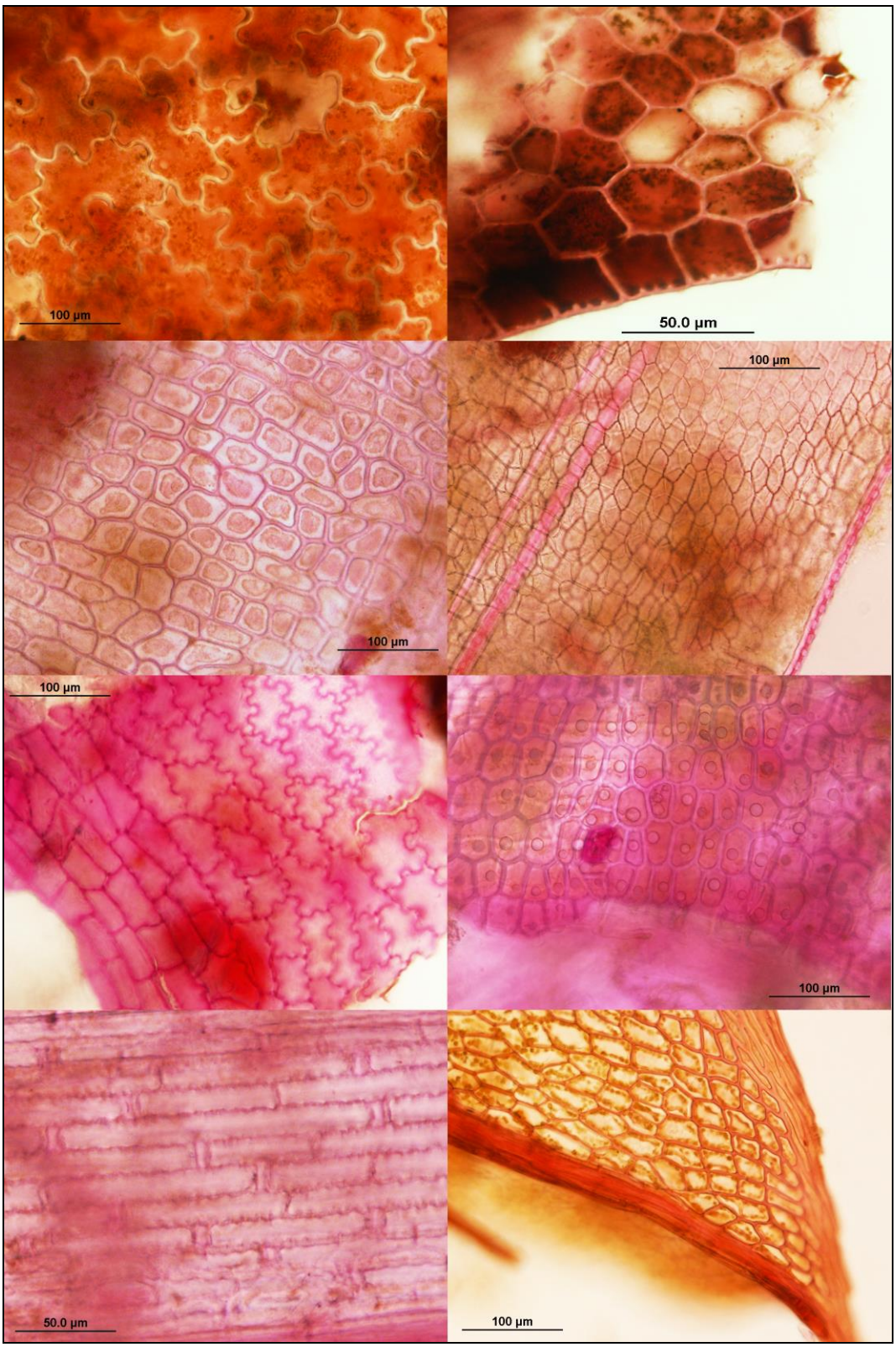

Figure 2.4. A selection of images from the plant cuticle database, demonstrating the morphological variety that occurs in the size, shape, and arrangement of the epidermal cells between species. First row, *Blechnum colensoi* (left) and Hymenophyllum *flabellatum* (right). Second row *Phyllocladis trichmanoides* (left) and *Rhopalostylus sapida* (right). Third row, *Ripogonum scandens* (left) and *Astelia banksii* (right). Fourth row, *Microstegium vimineum* (left) and *Bryum argenteum* (right). The red/purple hue of the fragments is due to the fuchsin dye that was used to stain the samples. All photographs by the author (2013).

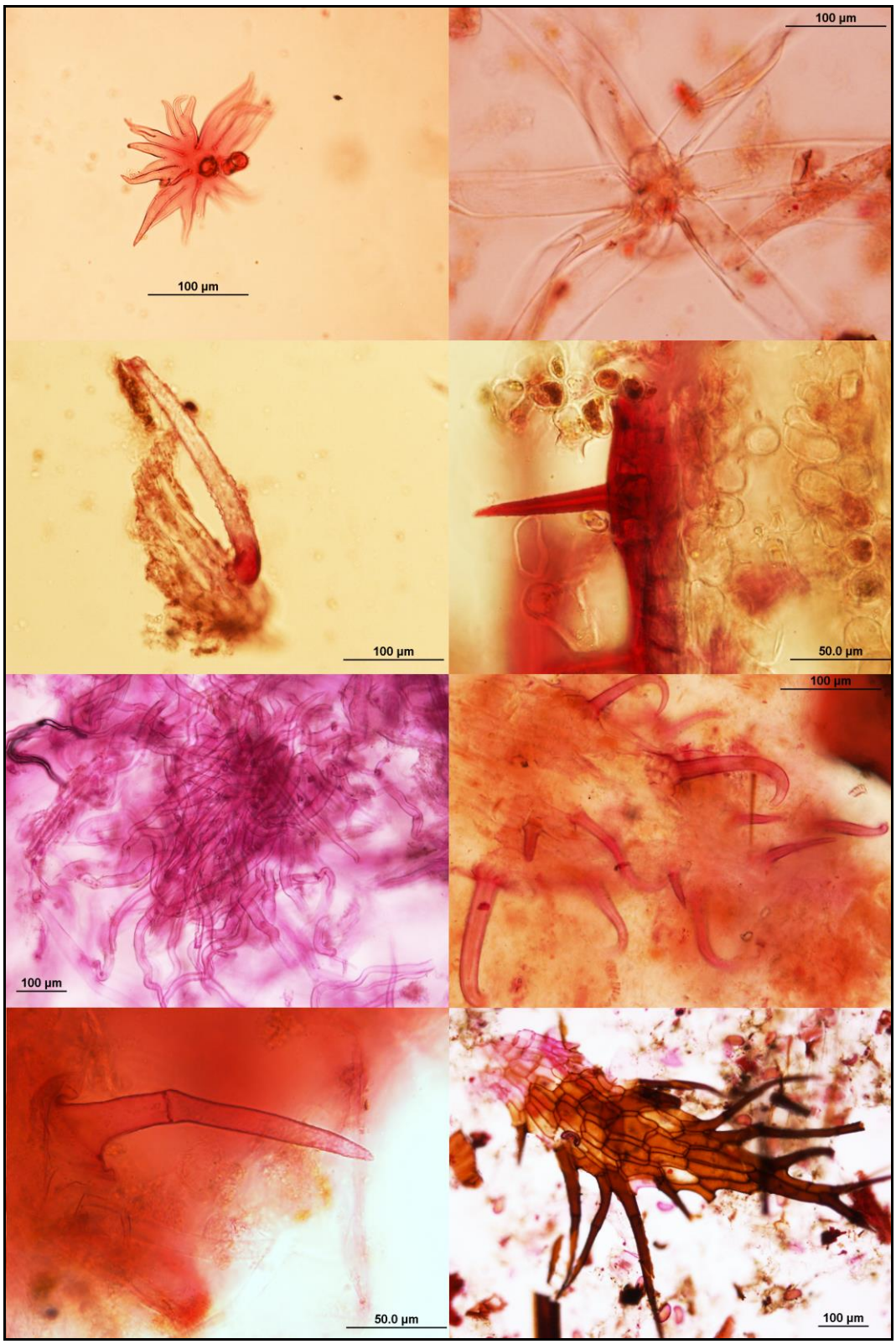

Figure 2.5. A selection of images from the plant cuticle database, demonstrating the morphological variety that occurs in the size and shape of the leaf hairs (trichomes) between species. First row, *Adiantum cunninghamii* (left) and *Pyrrosia serpens* (right). Second row, *Carpodetus serratus* (left) and *Melicytus ramiflorus* (right). Third row, *Olearia arborescens* (left) and *Pennantia corymbosa* (right). Fourth row, *Coprosma rotundifolia* (left) and *Microsorum pustulatum* (right). All photos by Author (2013).

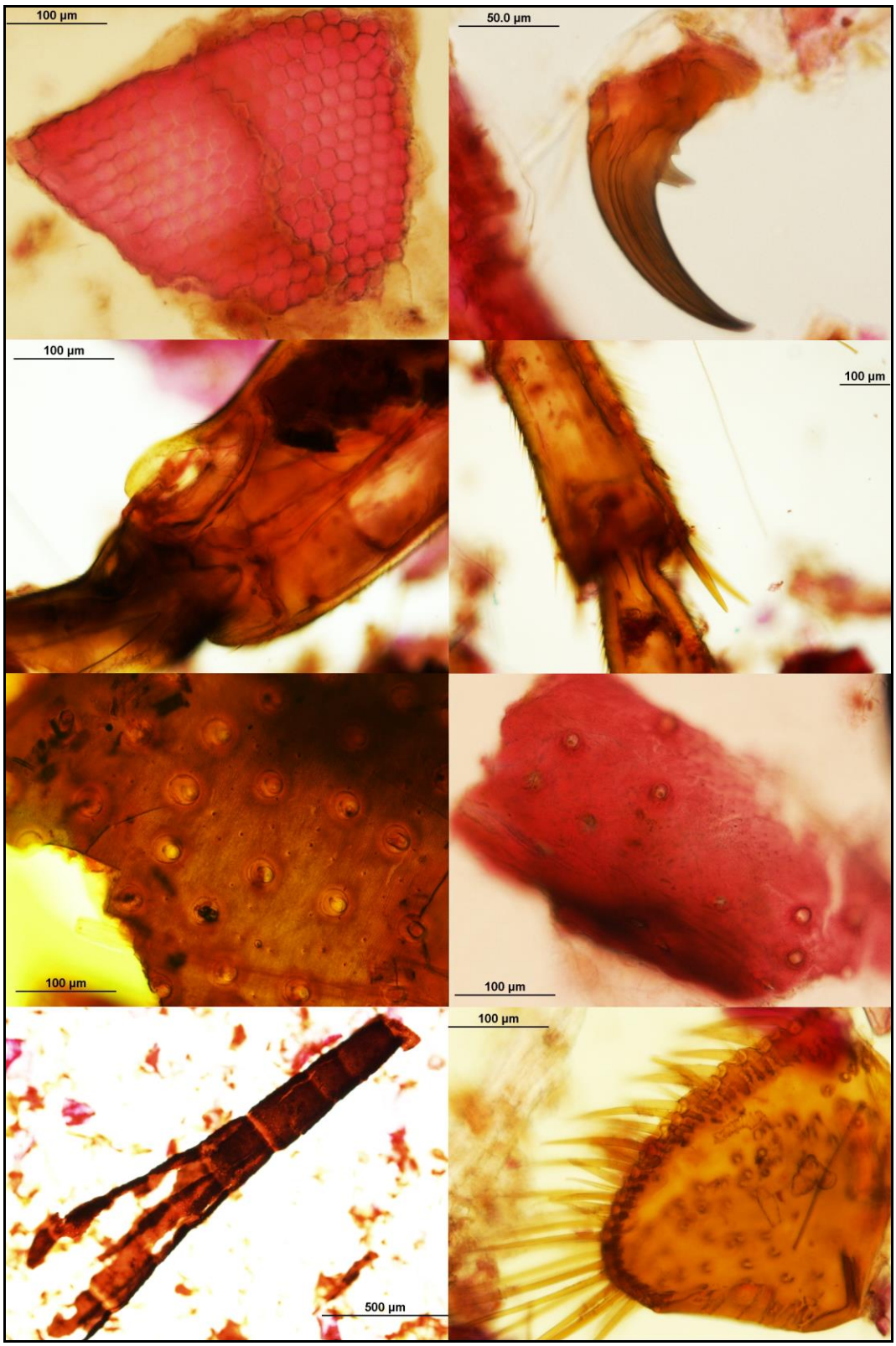

Figure 2.6. Invertebrate fragments are visually distinct from plant fragments under magnification. The following were photographed in the frass of wild *H. thoracica*. First row, part of a compound eye (left) and a piece of a tarsal claw (right). Second row, two intact leg joints (left and right). Third row, a piece of exocuticle (the rigid outer-layer of the exoskeleton) (left) and a piece of endocuticle (the pliable, inner-layer of the exoskeleton) (right). Fourth row, a piece of an antenna (left), and an unidentified exocuticle fragment (right). All photos by Author (2013).

2.3.3 The Diversity of Plant Species Consumed by Wild *H. thoracica*

In total, 43 *H. thoracica* were returned to the animal house facilities and produced frass. The captive wētā produced 107 pellets in the first 96 hours after capture, and 18 different plant species, from 13 different families, were identified in the frass (Table 2.1). Six additional tissue types were recognised, but could not be identified. The stomata and epidermal patterns of *Melicytus micranthus* and *Melicytus ramiflorus* appear almost identical when viewed under magnification, and I decided that I had probably misidentified one as being the other on some occasions. For analysis, I merged them into a single column '*Melicytus*'.

Table 2.1. Plant species that were identified in the frass of *H .thoracica*. An * indicates an invasive species

Family	Species
Lichens	
Parmeliaceae	*Parmelia*
Ferns	
Cyatheaceae	*Cyathea dealbata*
Hymenophyllaceae	*Hymenophyllum species*
Polypodiaceae	*Pyrrosia serpens*
Gymnosperms	
Podocarpaceae	*Dacrycarpus cupressinum*
	Dacrycarpus dacrydioides
	Podocarpus totara
	Prumnopitys taxifolia
Angiosperms	
Araliaceae	*Pseudopanax crassifolius*
Arecaceae	*Rhopalostylus sapida*
Myrsinaceae	*Myrsine australis*
Myrtaceae	*Kunzia ericoides*
Oleaceae	*Ligustrum sinense* *
Pennantiaceae	*Pennantia corymbosa*
Rousseaceae	*Carpodetus serratus*
Rubiaceae	*Coprosma rotundifolia*
Violaceae	*Melicytus micranthus*
	Melicytus ramiflorus
Unidentified Tissues	
	'big epiderm'
	'stellate'
	'chains'
	'pods'
	'wavy'
	'black droplets'

2.3.4 The Diets of Male and Female *H. thoracica*

The mean number of plant species identified in the frass differed between topographical zones, but not between the sexes (Figure 2.7). The mean number of plant species identified in the frass of male wētā from the terrace, the mid hillslope, and the upper hillslope zones were 6.87 (Std.Err ± 0.79), 4.6 (Std.Err ± 1.12), and 3.57 (Std.Err ± 0.53) respectively, and the mean number of plant species identified in the frass of female wētā from those same zones were 6.87 (Std.Err ± 0.77), 4.87 (Std.Err ± 0.64), 2.86 (Std.Err ± 0.74). One way ANOVA revealed that there was no significant difference in the number of plant species identified in the frass pellets produced by either sex, in any zone ($p = 1.0$, 0.82, and 0.45 for the plateau, mid hillslope, and upper hillslope zones), or in the percentage of individuals that produced fragments of any species ($p = 1.0$, 0.78, and 0.676 for the terrace, mid hillslope, and upper hillslope zones). One way ANOVA also revealed no significant differences in the number of fruit and seed, or invertebrate fragments produced by male and female wētā in any zone ($p > 0.05$ in all comparisons) except for the mid hillslope, where males produced significantly more fruit and seed fragments than females. This was the only difference detected between the sexes in any area, and therefore the fragment data for male and female wētā were grouped together for all further analyses.

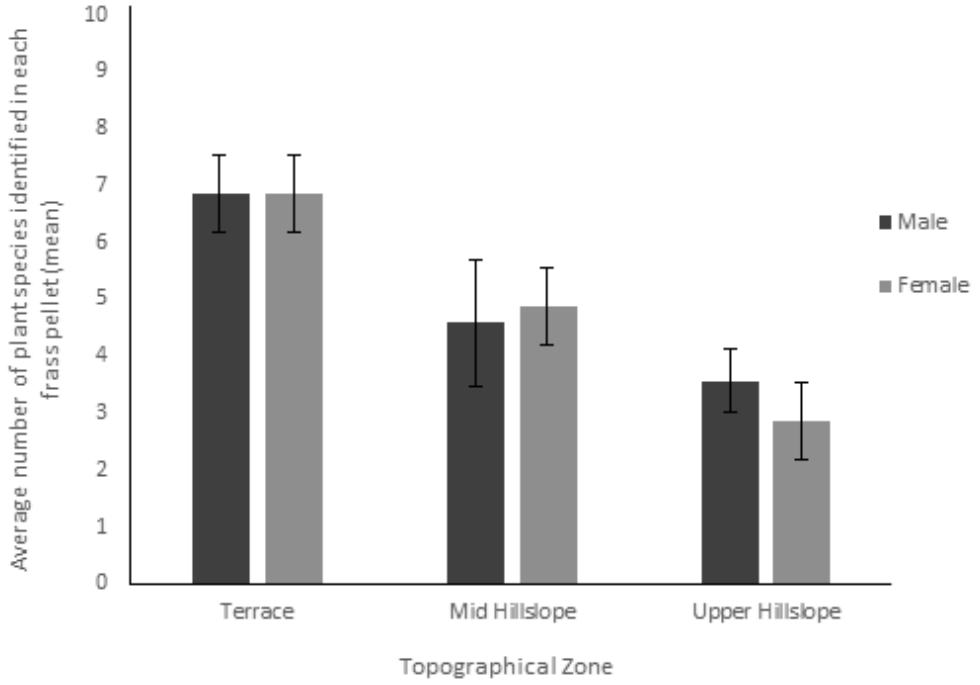

Figure 2.7. The mean number of plant species identified in the frass of male and female *H. thoracica* in each topographical zone, and SE.

2.3.5 The Total Composition of the Fragments Identified in the Frass of the *H. thoracica* from Each Sample Zone

The plants that were most highly represented in the frass of the wētā from the terrace were *P. taxifolia*, *D. dacrydioides*, and *Melicytus*, in that order, with total contributions to all identifiable fragments of 26.06 %, 21.33 %, and 10.85 % each respectively, followed by *C. rotundifolia* and *P. corymbosa* with contributions of 4.23 % and 3.94 % each respectively. These items, combined with fruit and seed tissues (18.02 %) and invertebrate fragments (5.96 %) accounted for 90.39 % of all fragments produced by the wētā from this zone (Figure 2.8 A).

The plants that were most highly represented in the frass of the wētā from the mid hillslope were *P. totara*, *K. ericoides*, *Melicytus*, and *P. taxifolia*, in that order, with total contributions of 10.89 %, 10.23 %, 9.67 %, and 3.21 % each respectively. These species, combined with fruit and seed tissues (28.29 %) and invertebrate fragments (7.03 %), accounted for 69.32 % of all of the fragments that were produced by these wētā. The unknown tissues 'chains' and 'stellate' were produced by one wētā each, but in large quantities (4.79 % and 3.89 % respectively) and 'pods' was produced in small amounts by two wētā (1 and 4 fragments each), but in such a large quantity by a third that it appeared to outrank all other tissues (12.9 %). If these outliers are discounted, the contribution of *P. totara*, *K. ericoides*, *Melicytus*, and *P. taxifolia* readjust to 13.89 %, 13.04 %, 12.33 % and 4.1 % respectively, and combined with fruit and seed tissues, and invertebrate fragments, account for 88.39 % of all of the fragments identified in the frass of the wētā from this zone (Figure 2.8 B).

The plants that were most highly represented in the frass of the wētā from the upper hillslope were *P. totara*, *K. ericoides*, and *C. serratus* with total contributions of 29.62 %, 18.92 %, and 4.39 % respectively. The unknown tissues 'chains' and 'wavy' were each produced by one wētā , but in great quantity and combined accounted for 11.62 % of all of the fragments from this area. If these outliers are excluded from the results, then the contributions of *P. totara*, *K. ericoides*, and *C. serratus* readjust to 33.52 %, 21.41 %, and 4.96 % each, and these three plants, combined with fruit and seed tissues and invertebrate fragments (which readjust to 11.77 % and 24.05 % respectively), account for 95.71 % of the fragments produced by the wētā from this zone (Figure 2.8 C).

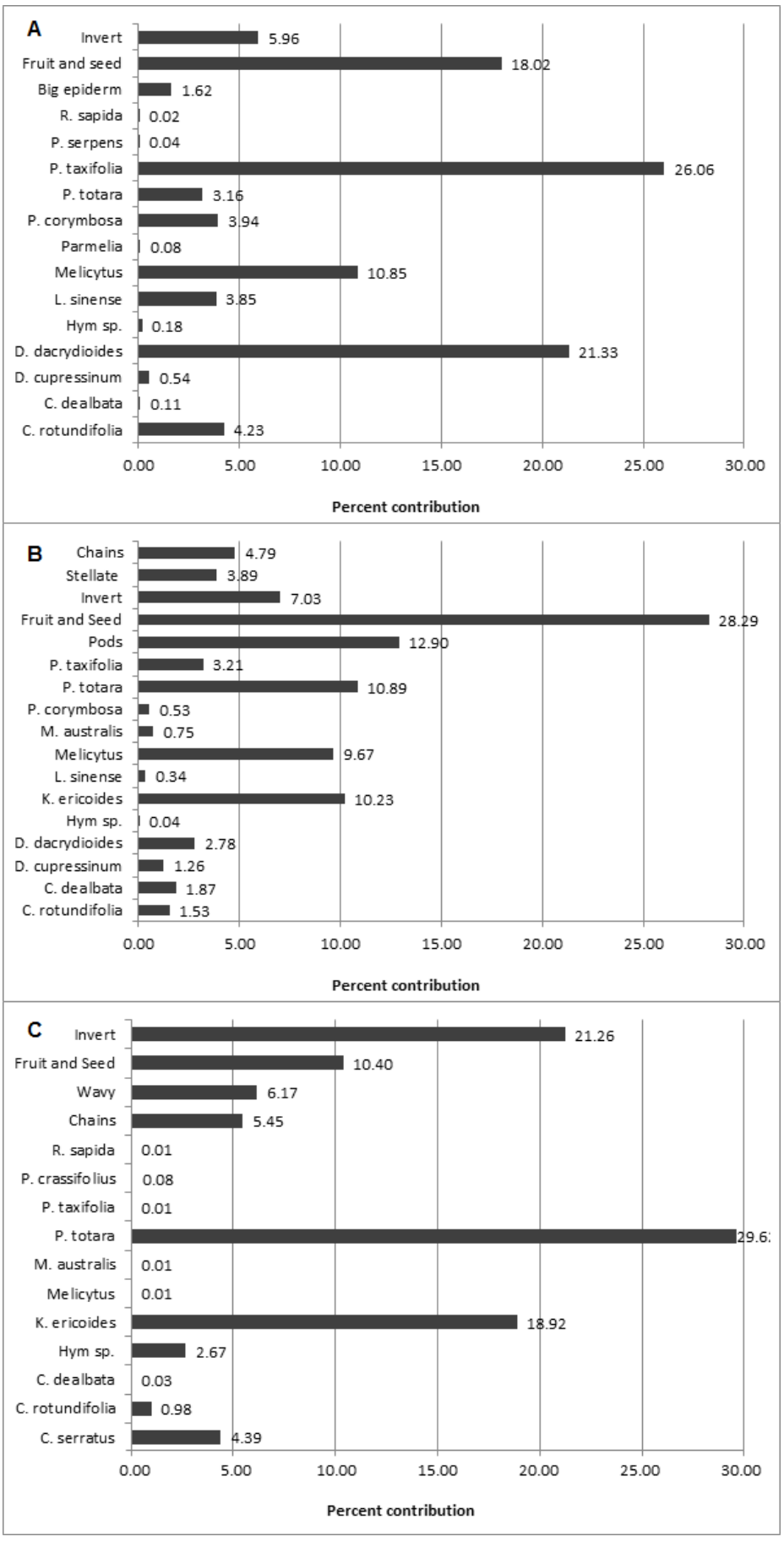

Figure 2.8. The composition of the faecal fragments identified in the frass of *H. thoracica* from (A) the plateau, (B) the mid hillslope, (C) and the upper hillslope.

2.3.6 Expected vs. Observed Fragment Counts

44 frass pellets were produced by the *H. thoracica* collected from the terrace, from which 20516 fragments were identified. A one-way, chi-squared test (d.f 12) revealed that there was a significant difference between the expected consumption of plant species (ground cover), and the observed consumption (fragment densities) of plants on the terrace ($p < 0.0000$). The plants that were most highly represented in the faecal fragments were *P. taxifolia*, *D. dacrydioides*, and *Melicytus* (Figure 2.9), all of which were more highly represented in the frass than predicted by their availability. The adjusted cover for each of these species was 24.50 %, 6.19 %, and 5.57 % respectively, which translate to predicted fragment counts of 5026, 1270, and 1142 (Appendix 2.2 A), but the observed fragment counts for each of these species was 5346 (*P. taxifolia*), 4377 (*P. taxifolia*), and 2227 (*Melicytus*). Conversely, other species in this area that had equal, or greater levels of ground cover, had far lower observed fragment counts than were predicted by their availability, such as *L. sinense* and *Selaginella*. *Ligustrum sinense* had an adjusted ground cover of 25.84 %, which translates to an expected fragment count of 5300, but only 790 *L. sinense* fragments were counted in total. *Selaginella* had an adjusted ground cover of 9 %, which translates to an expected total of 1828 fragments, but no *Selaginella* fragments were observed.

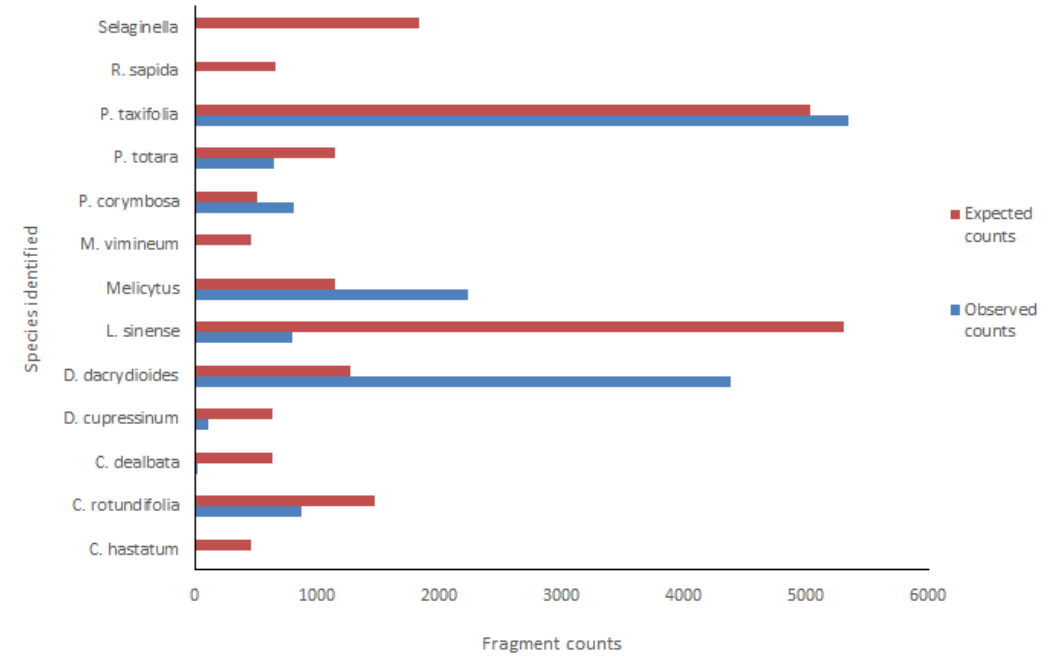

Figure 2.9. Expected vs. observed fragment counts, of all plant species with at least 5 % recorded ground cover at the terrace.

28 frass pellets were produced by the *H. thoracica* that were collected from the mid hillslope, from which 13101 fragments were identified. A one-way, chi-squared test (d.f 19) revealed that there was a significant difference between the expected consumption of the plant species present in this zone, and the observed consumption of those species ($p < 0.0000$). The plant species that were most highly represented in the faecal fragments of the wētā from the mid hillslope were *P. totara*, *K. ericoides*, and *Melicytus* (Figure 2.9.1), and the fragment counts for each of these species were higher than predicted by their availability. The adjusted ground cover for each of these species was 5.91 %, 3.94 %, and 6.11 % respectively, which translate to expected counts of 775, 516, and 800, but the observed counts for each of these species were 1820 (*P. totara*), 1709 (*K. ericoides*), and 1616 (*Melicytus*), more than double the expected (Appendix 2.2 B). However, other species in this area that had high levels of ground cover, had lower observed fragment counts than predicted by their availability, including *B. tawa*, *B. filiforme*, and *C. dealbata*. The adjusted ground cover for each of these species was 18.72 %, 8.87 %, and 5.91 %, respectively, which translate to expected fragment counts of 2453, 1162, and 775, but only 312 *C. dealbata* fragments were observed, and no *B. tawa* or *B. filiforme* fragments were observed.

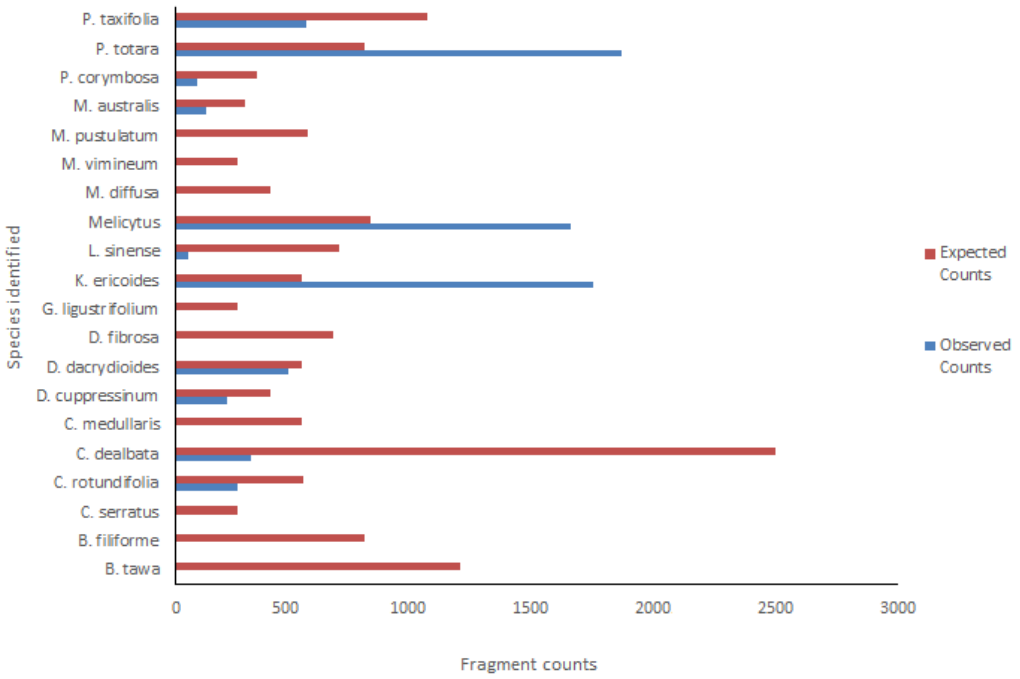

Figure 2.9.1. Expected vs. observed fragment counts, of all plant species with at least 5 % recorded ground cover at the mid hillslope.

35 frass pellets were produced by the *H. thoracica* collected from the upper hillslope, from which 16335 fragments were identified. A one-way, chi-squared test (d.f 16) revealed that there was a significant difference between the expected consumption of the plant species present, and the observed consumption of those species ($p < 0.0000$). The plant species that were most highly represented in the frass from this area were *P. totara*, *K. ericoides*, and *C. serratus* (Figure 2.9.2), and the fragment counts for these three species were all higher than predicted by their availability. The adjusted ground cover for each of these species was 20.55 %, 8.06 %, and 2.01 % respectively, which translate to expected fragment counts of 3356, 1316, and 329, but the observed fragment counts for each of these species were 5475 (*P. totara*), 3947 (*K. ericoides*), and 811 (*Melicytus*) (Appendix 2.2 B). Again, a number of plant species that were were equally, or more abundant in this area were consumed far less than predicted by their availability, including *B. tawa*, *C. dealbata*, and *Selaginella.* The adjusted ground cover for each of these species was 10.07 %, 10.07 %, and 8.06 % each respectively, which translate to expected fragment counts of 1645 for *B. tawa* and *C. dealbata*, and 1316 for *Selaginella*, but only 6 *C. dealbata* fragments were observed in the frass from this area, and no fragments of either *B. tawa* or *Selaginella* were observed at all.

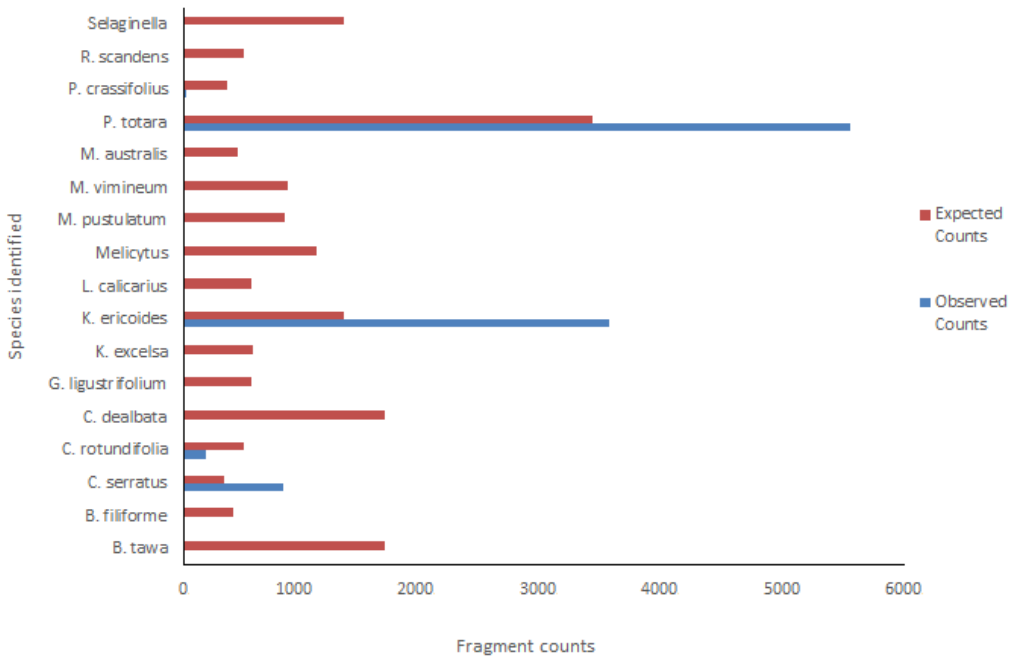

Figure 2.9.2. Expected vs. observed fragment counts, of all plant species with at least 5 % recorded ground cover at the upper hillslope.

2.3.7 Fruit, Seed, and Invertebrate Consumption

Although the composition of the plant community at the study site differs between areas, all three of the topographical zones where *H. thoracica* were collected had mature aniosperm and podocarp trees in their canopy, and therefore fruits, seeds, and the fleshy modified scales of podocarps, would have been available to the wētā from all three zones. All three areas would also have had some sort of macroinvertebrate community. However, the density of fruit and seed fragments, and invertebrate fragments in the frass was found to differ between areas. In general, wētā from the mid hillslope zone produced a lot more fruit and seed fragments in their frass than wētā elsewhere on the property, whereas wētā from the upper hillslope zone produced the most invertebrate fragments in their frass.

Fruit and seed tissues were present in the frass of 86 % of all of the captured wētā, but the mid hillslope wētā produced more fruit and seed fragments on average than weta from either the terrace, or the upper hillslope (Figure 2.9.3). The proportion of identified fragments that were derived from fruits and seeds was similar for the terrace wētā and the upper hillslope wētā, with means of 11.10 % (Std.Err. ± 3.38) for the terrace, and 9.88 % (Std.Err. ± 4.15) for the upper hillslope. However, on average 34.86 % (Std.Err. ± 9.06) of the faecal fragments identified in the frass pellets produced by the mid hillslope wētā were from fruits and seeds. One way ANOVA showed that location had a a significant effect on the density of fruit and seed fragments in the frass ($F = 5.76$; $p = 0.006$), and Tukey's post hoc-comparison revealed that the density of fruit and seed fragments produced by the wētā from the mid hillslope was signficantly different to both the terrace ($p = 0.015$) and the upper hillslope ($p = 0.013$).

Invertebrate fragments were present in the frass of 93 % of the captured wētā, and the mean concentration increased step-wise from the terrace, to the mid hillslope, to the upper hillslope zone (Figure 2.9.3). The mean concentration of invertebrate fragments in the frass increased from 5.29 % (Std.Err. ± 2.22) at the terrace, to 16.67 % (Std.Err. ± 7.74) at the mid hillslope, to 24.05 % (Std.Err. ± 6.26) at the upper hillslope. One way ANOVA did not detect significant differences in invertebrate consumption between zones ($F = 2.98$; $p = 0.06$), although Tukey's post-hoc comparison revealed an almost-significant difference in the quantity of invertebrate fragments prdoduced by the terrace wētā and the upper hillslope wētā ($p = 0.052$).

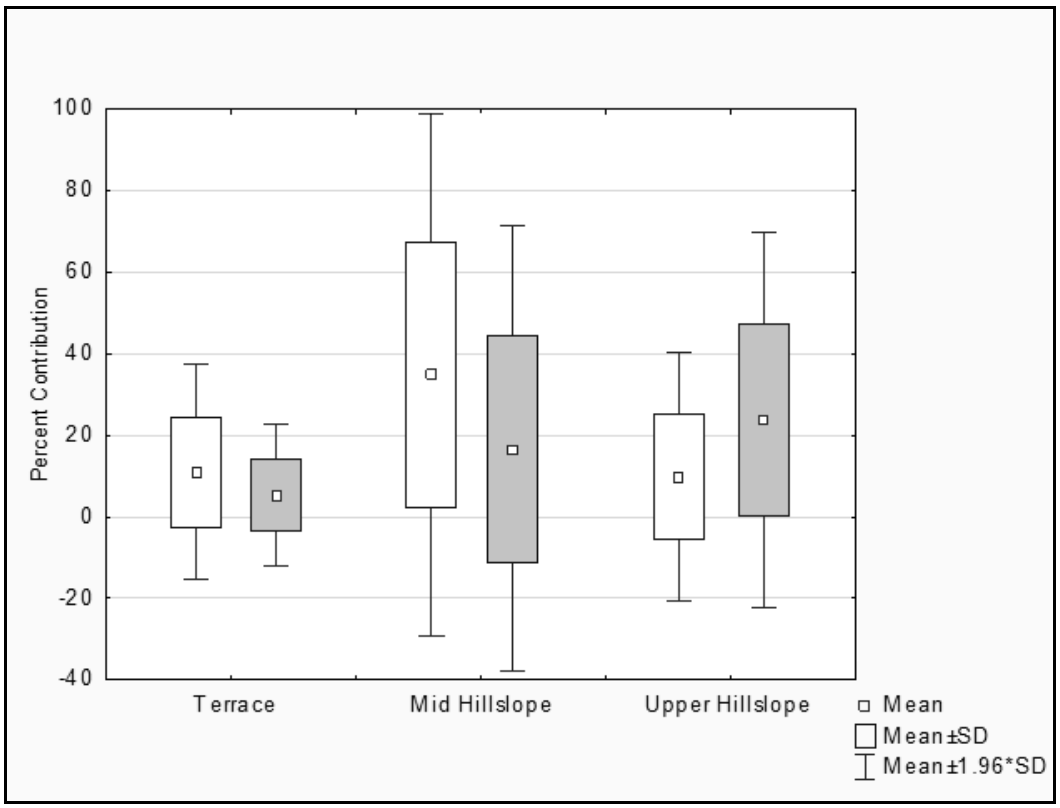

Figure 2.9.3. The total contribution that fruit and seed (white) and invertebrate (grey) fragments made to all of the identifiable fragments identified in the frass of the *H. thoracica* from each of the sample zones.

2.3.8 Solvent Extraction of Leaf Lipids and Oils

In the solvent extraction, Group 1 was composed of the leaves of plants that appeared to be preferred by the wild *H. thoracica* at the study site, and included *K. ericoides*, *P. corymbosa*, *P. taxifolia*, *P. totara*, *M. micranthus*, *M. ramiflorus*, *C. rotundifolia*, and *C. serratus*, whereas Group 2 was composed of plants that were common at the study site, but which were not eaten, and included *C. dealbata*, *D. cupressinum*, *D. fibrosa*, *G. ligustrifolium*, *L. sinense*, *M. australis*, *M. vinimeum*, and *Selaginella*. The leaves of the preferred group of plants had a mean concentration of lipids and oils of 3.659 mg/g^{-1} (Std.Err. ± 1.6 g), whereas the non-preferred plants had a mean concentration of leaf lipids and oils of 1.268 mg/g^{-1} (Std.Err. ± 0.29 g) (Table 2.4). *Kunzia ericoides*, in Group 1, was a high-outlier, with a lipid/oil concentration more than three times higher than the next highest ranking plant in that group (which was *P. taxifolia* with 3.95 mg/g). If *K. ericoides* is removed, the mean concentration of hexane-soluble materials in Group 1 drops to 2.12 mg/g^{-1} (Std.Err. ± 0.48 g), which is still 1.7 times higher

than that of Group 2. However, there is overlap between the two groups, and ANOVA did not detect a significant difference ($F = 2.41$; $p = 0.14$).

Table 2.2. The concentration of lipids and oils (mg/g^{-1}) in the leaves of eight plants that were readily eaten by wild *H. thoracica* (Group 1), and eight plants that were highly available, but which were not eaten (Group 2).

Group 1	Lipids + oils (mg/g^{-1})
C. rotundifolia	1.65
C. serratus	2.54
K. ericoides	14.45
M. micranthus	1.12
M. ramiflorus	1.18
P. corymbosa	3.62
P. taxifolia	3.95
P. totara	0.76
Mean	3.659 (Std.Err. ± 1.6)
Group 2	**Lipids + oils (mg/g^{-1})**
C. dealbata	1.99
D. cupressinum	1.63
D. fibrosa	1.62
G. ligustrifolium	0.22
L. sinense	0.42
M. australis	2.6
M. vimineum	0.81
Selaginella	0.96
Mean	1.268 (Std.Err. ± 0.29)

2.4 Discussion and Conclusions

This experiment set out to expand upon the existing body of data concerning the ecology of the Auckland tree wētā *H. thoracica* by answering the questions;

- What do *H. thoracica* eat in the wild?
- Are *H. thoracica* better described as herbivores, or omnivores?
- Do *H. thoracica* forage randomly, or selectively?
- Do *H. thoracica* preferentially select the leaves of plants that have high concentrations of lipids and oils?

The data that were gathered here, have provided insight into each of these questions, and revealed a great deal about the diet of *H. thoracica* in the wild, and uncovering this information has in turn opened up new questions, and new lines of future inquiry relating to these animals.

2.4.1 *Hemidena thoracica* is an Extreme Polyphage, and Consumes a Diet Primarily Composed of the Leaves of Native Plants

Insect herbivores are often grouped into categories based on their degree of dietary specialisation (Ali & Agrawal, 2012). When restricted to feeding on one or a few closely related species from the same genus, they are referred to as monophagous, when they feed on multiple species within the same family, they are referred to as oligophagous, and when they feed on multiple species from multiple families they are referred to as polyphagous (Ali & Agrawal, 2012). The *H. thoracica* in this study had consumed a wide variety of leaves, mostly from native species of angiosperms and podocarps. In total, 18 species of plants, from 13 families, were positively identifed in the frass of the *H. thoracica* I captured from the study site at the Waingaro Forest Reserve, with *P. taxifolia, K. ericoides, P. totara, D. dacrydioides*, *Melicytus*, *P. corymbosa*, and *C. rotundifolia*, being the most highly represented (in that order). The high number of different plant species whose leaves were utilised by the *H. thoracica* in this study, indicates that this animal is an extreme polyphage, and naturally utilises a wide variety of food sources.

2.4.2 *Hemideina thoracica* are Omnivores

Invertebrate fragments were present in the frass of 93.2 % of the *H. thoracica* that were captured from the study site, and invertebrate fragments made up a total of 11 % of all the fragments that were identified, although in some areas the overall density of invertebrate fragments was higher than this. This indicates that *H. thoracica* are more accurately described as omnivores, rather than herbivores. My results are very similar to the findings of Lodge (2000) who discovered that invertebrate fragments occurred in 87 % of all of the frass of wild *H. maori* from the Rock and Pillar Range (Otago) and made up 10 % of all identifiable fragments in their study. In my study, inverterbrate consumption also appeared to increase stepwise from the terrace upwards. The actual invertebrate-fragment component of the wētā frass from each zone was 5.96 %, 7.03 %, and 21.26 % at the terrace, the mid hillslope, and the upper hillslope respectively, and the difference between the terrace tree wētā and the upper hillslope tree wētā was on the border of being statistically significant ($p = 0.052$). If the upper hillslope wētā were consuming more invertebrates than wētā elsewhere, then there may be several explanations for an increase in predatory behaviour. The terrace and the mid hillslope have

diverse, and very dense, sub-canopy and shrub layer vegetation. On the other hand, the upper slope and hillcrest zones near the peak of the property have a much more open sub-canopy, with little shrub-level cover in many areas. The difference in sub-canopy diversity and density between the lower and upper zones raises two possibilities. The first is that the reduced density of the understory vegetation in the upper hillslope area could mean that insects have less opportunity to hide or escape from foraging tree wētā, making them more accessible as a food source. The other possibility is that the reduced complexity of the foliage in the upper hillslope area, and the high density of unpalatable species, could mean that wētā in this area struggle to construct a satisfactory diet from the plants available, and so engage in more predatory behaviour to compensate.

2.4.3 *Hemideina Thoracica* are Selective Foragers

Their diet is broad, and probably quite flexible, but they do not appear to feed at random. Comparing the observed density of plant fragments in the wētā frass, against the expected counts (as predicted by the ground cover of the species) showed that in any area a small handful of plants were typically consumed in quantities equal to, or greater than, those predicted by their groundcover. This may indicate that some species are consumed whenever they are encountered, and thus could be considered highly palatable to the *H. thoracica* of the site. On the other hand, many plant species that were present in a much greater density were not eaten at all, or were eaten much less than would be predicted if *H. thoracica* displayed a low degree of discrimination when feeding.

For example, *L. sinense* occurred in all ten recce plots recorded on the terrace, and had an average ground cover of 65 % in that area (with an actual range of 50 % to 75 %), but only made up 3.85 % of all of the faecal fragments identified in the frass produced by the wētā from this zone. It is impossible that the wētā living on the terrace were not regularly coming into contact with *L. sinense* leaves, the *L. sinens*e in that area is simply far too dense to avoid contact, and therefore, *H. thoracica* must reject *L. sinense* leaves as a food source. Other highly abundant species that were almost completely absent from the frass were grasses and lycopods (*M. vimineum* and *Selaginella*), all of the ferns, and the angiosperms *G. ligustrifolium* and *B. tawa*. *Microstegium vimineum* and *Selaginella* were common ground cover species at the terrace and upper hillslope, but were completely absent from the frass in either area, and both tree ferns and

other fern species were common in the sub canopy, the shrub layer, and as epiphytes, in all three zones, especially at the mid hillslope and upper hillslope areas. However, of the 43 *H. thoracica* that produced frass after capture, < 40 % from any zone produced fragments from any fern species, and only one individual produced frass that was > 1 % fern fragments by composition. This one pellet was produced by a male wētā from the mid hillslope, and contained a moderate number (300) of *C. dealbata* fragments. *Geniostoma ligustrifolium* and *Beilschmedia tawa* were both abundant from the mid hillslope upwards, *G. ligustrifolium* was common in the under story and shrub layer, and *B. tawa* contributed a signifcant percentage to the canopy cover in the mid hillslope zone, and was the major contributor to all of the leaf litter in this area, but no fragments of either species were discovered in the frass.

Hemideina thoracica appear to discriminate between available food sources, and are therefore selective foragers. Dewhurst (2012) performed a fragment analysis on the frass of *H. thoracica* collected from three different locations throughout the Western foothills of the Tararuas in the lower North Island. They recorded the vegetation in a 5 m^2 plot around the daytime refuge of each wētā, and then compared the vegetation composition of each plot to the composition of the plant fragments present in the frass produced by each wētā (recorded as simply present or absent). They found that the wētā frequently did not consume the plants that they were most likely to encounter first, after leaving their galleries (the plants nearest the entry holes), causing them to also conclude that *H. thorac*ica feed selectively (Dewhurst, 2012).

2.4.4 *Hemideina thoracica* May Preferentially Select Leaves with High Lipid Concentrations

The percentage of digestible material is higher in some plants than others (House, 1969), and being able to distinguish between high and low digestibility plants could have important implications in foraging optimally (netting the greatest energy gain per unit of time spent foraging). Experimental studies have shown that feeding on lipids results in greater growth and reproduction in arthropods, and that arthorpods (particularly predatory and omnivorous arthropods) may be more limited by lipids than nitrogen (Mayntz & Toft, 2001; Manyntz *et al*., 2005; Raubenheimer *et al*., 2007). Extracting the oils and lipids from the leaves of preferred and non-preferred plant species showed that the plants that the *H.*

thoracica in my study were eating had a higher mean concentration of lipids and oils in their leaves than other species that were equally, or more, abundant, but which were not consumed. Group 1 had a lipid/oil concentration three times higher than group 2, and four plants in group 1 (*K. ericoides*, *P. corymbosa*, *P. taxifolia*, and *C. serratu*s), fully half the group, had leaf lipid scores that were higher than every plant in group 2. Group 1 had one very high outlier (*K. ericoides*), but even after this had been removed, the mean concentration of leaf lipids and oils in Group1 was still almost double that of Group 2. One way ANOVA did not detect a significant difference between the groups, but the groups were small, and there was some overlap between the values in each group. I am certain that increasing the sample size would result in a lower p-value. For the preferred group, I had to include plants that were highly represented in the faecal fragments, and for the non-preferred group I had to use plants that were not highly represented in the faecal fragments, but which were abundant enough in the area that the wētā could realistically have been encountering them. This limited the number of species I could include in the extraction. If I were able to increase the sample size for both groups, I am confident that a follow up test would show a significant difference. More study is warranted in this matter.

Multiple faecal fragment analyses have been performed on the closely related mountain stone wētā *H. maori* (Lodge, 2000; Joyce, 2002; Wilson, 2004). These studies were all performed in the Rock and Pillar ranges of the Southern Alps, and they found that *Anisotome imbricata*, *Anisotome inconspicua*, *Celmisia viscosa*, *Celmisia brevifolia*, *Helichrysum selago, Kelleria villosa*, *Leptospermum scorparum, Poa colensoi*, *Podocarpus nivalis,* and *Raoulia hectori* were eaten more frequently by *H. maori* than other plants which were more abundant in the same area. Most of the above plant species have high concentrations of lipids in their leaf tissues compared to other plants on the Rock and Pillar ranges (Bliss & Mark, 1974), and *H. maori* may therefore select for lipid rich food sources as well. The results of my study, combined with the findings of Lodge (2000), Joyce (2002), and Wilson (2004), provide evidence that the concentration of lipids and oils in the leaves is a significant factor in determining the palatability of leaves to tree wētā, which appear to preferentially consume plants with high concentrations of these nutrients.

2.4.5 *Hemideina thoracica* May Forage on the Forest Floor

Initially, after counting and identifying all of the faecal fragments, I attempted to compare the fragment composition of the frass against the vegetation composition of each of the six vertical tiers of the forest, to determine where in the forest column the wētā were doing their foraging. However, no correlations could be found between the composition of the fragments in their frass, and the composition of the vegetation at any one tier. The confounding factor was that although they were eating many leaves from canopy trees, particularly *P. taxifolia*, *P. totara*, and *D. dacrydioides*, the composition of their frass was frequently far more diverse than the plant community of the canopy, and often included the leaves of smaller plants that were only growing in the understory and shrub layer, like *Melicytus*, *Pennantia*, and *Coprosma* species. The maximum dispersal rate of tree wētā has been estimated to be about 12.07 ± 1.57 m/night^{-1} (Kelly, 2006b). Unless their actual nightly dispersal rate is substantially higher than this, then it is unlikely that any wētā climbed down from their gallery to the ground, travelled the distances between 3-7 different trees, climbed up and down each tree (some of which were greater than 25 m tall), and then returned to their gallery, all in a single night. How the *H. thoracica* at the study site were simultaneously foraging on multiple plants that were growing up to 30 m apart by height was baffling, until it occurred to me that relatively fresh leaves from all of the plants growing in any plot, at any height, could all be encountered on the forest floor beneath those plants. When I transformed the vegetation coverage data to represent the theoretical availability of different leaves on the forest floor, it revealed a number of strong, positive correlations between the fragment composition of the frass, and the leaf fall areas of a small number of common species.

Another factor that influenced this theory was the fact that down on the terrace, approximately two thirds of the wētā captured (72 %) were extracted from the trunks of live *L. sinense*, at around breast height, but the most frequently consumed plants in that same area were *P. taxifolia* and *D. dacrydioides*. The latter two species are both tall canopy trees, and in that area grow to heights in excess 25 m (tier 1), whereas very few of the *L. sinense* in this same area were taller than 3 m (tier 4). It is implausible that these wētā climbed from the *L. sinense* they were living in, straight up into the branches of the *D. dacrydioides* or

P. taxifolia overhead, which they were eating. This leaves two possibilities, that they descended to the ground, travelled to the base of the larger trees, and then climbed them in search of food before returning, or that they descended to the ground, and then foraged fresh litter off of the forest floor.

In the wild, resources are distributed in a patchwork in three dimensions, and optimal foraging theory predicts that the foraging behaviour that is most enlarged should be the one that optimises the utilization of time and energy (e.g. that which results in the greatest net-gain of energy per unit of time spent foraging, while accounting for the risk/reward ratio of the strategy) (MacArthur & Pianka, 1996). If *H. thoracica* forage in the canopy, the travel time (from tree to tree) would be high, meaning prolonged exposure to the vertebrate predators that eat tree wētā, and a high risk/reward ratio for any bout of foraging, plus every minute of time spent in transit between trees, is essentially wasted. On the other hand, if *H. thoracica* feed on the forest floor and in the undergrowth, then they could easily encounter a high diversity of different leaves, as well as fruits and seeds (fallen to the ground), in a much shorter space of time, by simply travelling in a line from their gallery for a relatively short distance, before returning again. This would result in less wasted time, optimising their utilisation of time and energy, and would also significantly reduce the amount time that they are exposed to predators and other environmental stresses.

Another observation that was brought to my attention, and which may support this theory, concerns the fact that *B. tawa*, though a common canopy tree and a large contributor to the leaf litter, was not eaten at all. The leaves of this species do not fall to the ground fresh and then wither, they wither on the plant, and then fall to the ground dry. In captivity I have observed that *H. thoracica* will reject plant materials once they are no longer fresh (usually 48 -72 hours) so their food needs to be changed regularly. If *H. thoracica* do feed on the forest floor, then virtually all of the *B. tawa* leaves they encounter will be dead and dry, and if *H. thoracica* in the wild also reject decomposed food if fresh food is also available, then *H. thoracica* foraging on the forest floor would reject the *B. tawa* leaves they encounter.

Mirams (1957) investigate the factors that affect kauri (*Agathis australis*) regeneration in six different successional-stage communities in the Waitakere ranges. They discovered that in all six communities, an animal was destroying a large number of kauri seeds on the ground before they could germinate. They

trapped a number of *H. thoracica* from around the study sites, using pitfall traps. They then fed these wētā on kauri seeds in a laboratory, and successfully matched the bite-marks on the laboratory seeds, to those on partially consumed seeds from the field. The fact that *H. thoracica* have also been recorded devouring large numbers of kauri seeds off of the forest floor at multiple locations supports my theory that *H. thoracica* frequently forage on the ground.

2.4.6 Limitations of this Study

As long as sampling is random, all of the frass pellets are processed the same way, and the system of identification and quantification is consistent, then faecal fragment analysis is accurate at identifying the diet of a group of animals that handle, digest, and degrade cuticle fragments to the same degree (Wilson, 2004). The methods of this study meet these criteria. While it has been observed that some plant species fragment more easily than others (Wilson, 2004), I have observed that most plants produce a large number of fragments in the frass of *H. thoraci*ca, even if the quantity consumed is small. While building my reference library, I observed that even plants that were only nibbled on very lightly, still produced dozens of identifiable fragments in the subsequent frass. I propose that if the sample size is large enough, and a great enough quantity of fragments are identified, then variable fragmentability should have a minimum effect on the overall image that is produced. In this experiment, 107 frass pellets, from 43 individual wētā, were processed and analysed, from which 50,000 individual fragments were identified and counted. Therefore I propose that this limitation would not have had a significant impact on the overall image of the diet of *H. thoracica* that resulted.

The other factor that may limit the accuracy of this study is the fact that a mortar and pestle were used to break down the frass pellets into a solution that could be passed through a paper filter. It is possible that the grinding process, though not vigorous, further fragmented existing fragments, changing the representation levels of some types. In creating my reference library, I fed some plants directly to the *H. thoracica* and then processed their frass, but to speed the process, I also pulverised samples of other plants manually with a mortar and pestle, and then transferred samples of the pulp onto slides for photography. I observed that hand-processed samples typically contained fragments that were much larger and coarser than those in wētā 'processed' samples (personal

observation). The alimentary canal of a tree wētā appears to be a more effective machine for grinding and reducing plant material into small fragments than a mortar and a pestle. This is not surprising considering the complex series of mechanical and chemical digestive processes that consumed leaves are exposed to as they pass through the wētās alimentary canal (Maskell, 1927). Therefore I do not consider it likely that my processing method significantly altered existing fragment ratios.

2.4.7 Suggestions for Future Research

While this study desmonstrated that some plants are recjected by *H. thoracica* in the wild as food sources, it could not fully quantify why this was the case. Most of the unpalatable species had a lower concentrations of lipids and oils than many of the preferred plant species, however, some unpalable plants had lipid and oil concentrations that were comparable to those of the preferred group. There must, therefore, be additional factors involved in determining preference. Toxic plant secondary metabolites strongly influence the feeding behaviour of most leaf-eating generalists (Raubenheimer, 1992; Behmer *et al*., 2002; Wiggins *et al*., 2006; Nersesian *et al*., 2011, 2012), and probably also factor into the foraging decisions of tree wētā. Determining which metabolites make plants unpalatable to foraging wētā, and whether or not these metabolites are particularly noxious to wētā, or more of a general herbivory-deterrant, would be valuable in increasing our understanding of the natural feeding behaviour of this animal.

The results of the faecal fragment analysis also indicated that there is a high *H. thoracica* may forage more often on the forest floor than has previously been recognised. This could be explored with a tracking study. Tree wētā galleries could be located, or artificial refuges could be attached to trees, and once colonised, the nightly movement patterns of the inhabitants could be followed either by filming them, or using a stain and tracking paper. If the study were performed in captivity, then other elements could also be factored into the analysis such as whether condition/body fat affects how frequently they forage, or whether the smell of vertebrate predators alters how they forage. Identifying where tree wētā actually go to forage, and if the presence of predators affects their normal foraging behaviour, would provide data on means by which introduced mammalian predators might impact tree wētā other than by direct predation.

2.5 Conclusions

The faecal fragment analysis method is considered one of the most accurate methods for assessing the diets of wild animals that are difficult to observe feeding, and the observations made in this study have revealed a great deal about the diet of *H. thoracica*. *Hemideina thoracica* are both frugivores and omnivores in the wild, and fruits and seeds appear to make up a significant proportion of their diets in the wild, whereas invertebrates are a smaller, but common component of their overall diet. They are discriminative foragers, and the concentration of lipids and oils in the leaves may be one of the chemical cues that they use to discriminate between available plant species that they encounter. It is also possible that they do more of their foraging on the forest floor than has been previously recognised. To summarise, the data gathered in this analysis suggests that *H .thoracica* are extreme polyphages, they are strongly discriminative feeders, and are naturally omnivorous.

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3 Chapter 3: Nutrient Balancing and Macronutrient Utilisation in the Tree Wētā *Hemideina thoracica*

3.1 Introduction

Tree wētā are large, flightless, nocturnal insects, and are an iconic component of the fauna of New Zealand. Tree wētā are grouped in the Order Orthoptera, which also includes the grasshoppers (Acrididae, MacLeay, 1918), crickets (Gryllidae, Laicharding, 1781), and katydids (Tettigoniidae, Kraus, 1902). Tree wētā numbers have declined heavily, due mostly to predation by introduced, r-selected, mammalian predators, particularly black rats (*Rattus rattus*, Linnaeus, 1758), ferrets (*Mustela furo*, Linnaeus, 1758), and hedgehogs (*Erinaceus europaeus*, Linnaeus, 1758) (Sherley, 1998; Innes, 2005; Jones & Sanders 2005; King & Murphy, 2005; Ruscoe & Murphy, 2005; Ruscoe *et al*., 2012), and current tree wētā population densities may be less than 10 % of their pre-human numbers (Watts *et al*.,2011). As they are small, nocturnal foragers, little is presently known about many of the most basic aspects of the ecology of these animals, and because of this, a foremost objective for restoration ecologists in New Zealand should be gathering as much information as possible about individual species of wētā, particularly information concerning their ecology in the wild (Minards, 2011). Developing a better understanding of the functional and nutritional ecology of these animals would be valuable in effectively determining whether they are at risk of further decline in the near future, and developing effective conservation and rehabilitation strategies for threatened wētā species.

Nutritional ecology is the trophic branch of functional ecology (Raubenheimer & Boggs, 2009) and aims to explain ecological phenomena with reference to organismal-level traits (Raubenheimer *et al.* 2009; Raubenheimer & Boggs, 2009). Most ecosystems are nutritionally heterogeneous, and resources are commonly distributed in a three dimensional patchwork throughout the environment (MacArthur & Pianka, 1996), and because of this, the nutrients ingested by any animal foraging can be imbalanced in time or space. There is now a significant body of evidence that demonstrates that animals can compensate for nutrient imbalance by ingesting a range of resources, and many animals demonstrate a strong ability to obtain an optimal diet by feeding on multiple,

incomplete food sources to different extents (Fryxell & Doucet, 1991; Cohen, 2001; Fagan *et al*., 2007; Behmer, 2009). The percentage of digestible material is higher in some plants than others (House, 1969), and being able to distinguish between high and low digestibility plants could have important implications in foraging optimally (netting the greatest energy gain per unit of time spent foraging). Therefore, when provided with the opportunity, an animal should select the diet that provides the greatest reproductive benefits, referred to as the 'nutritional target', which can be expressed as a ratio of protein to carbohydrates (P:C). This process, referred to as 'nutrient balancing' has been demonstrated in a number of invertebrates, including grasshoppers (Bernays & Bright, 1993; Raubenheimer & Simpson, 2003), locusts (Simpson & Raubenheimer, 2000) cockroaches (Cohen, 2001), spiders (Mayntz & Toft, 2001; Mayntz *et al*., 2005), caterpillars (Lee *et al*., 2006), beetles (Raubenheimer *et al*., 2007), and the Wellington tree wētā *H. crassidens* (Wehi *et al*., 2013).

In Chapter Two, fragment analysis of the faeces (referred to as 'frass') of the Auckland tree wētā *H. thoracica* from the Waingaro Forest Reserve showed that the diet of that population was dominated by leaves from at least 18 different species of plants. However, fragments from other invertebrates were also present in the frass of 93 % of all individuals, and made up 11 % of all of the fragments identified. This indicated that they are also naturally omnivorous, and a smaller component of their diet is composed of protein obtained by eating other insects. If these individuals were feeding optimally for this species, and this composition reflects the typical, natural diet of *H. thoracica*, then *H. thoracica* should only require a relatively small amount of protein in their diet to achieve optimal physical condition. If this hypothesis is accurate, then we would expect that *H. thoracica* provided with two or more foods with variable protein to carbohydrate ratios (P:C) will select a diet that is rich in carbohydrates. Many insects are nitrogen limited (Mattson, 1980), and it has been proposed that tree wētā are nitrogen limited also (Dewhurst, 2012). If this is correct, then the protein that *H. thoracica* do consume in the wild may be an important source of dietary nitrogen, and if this is accurate, then we would expect *H. thoracica* to utilise the protein they eat with a high level of conversion efficiency (the percent of digested material that is successfully converted into biomass). Whether or not wild *H. thoracica* feed to achieve a specific nutritional target, and how efficiently they

utilise the macronutrients they consume, can be explored by combining the geometric and gravimetric methods of nutritional analysis.

The geometric method measures changes in two or more related variables over time as a ratio (Simpson & Raubenheimer, 1995, 2012), and is based on the logic of state-space geometry, where the measured variables are expressed and related to each other in a geometric space, such as a scatterplot. These variables may include the consumption of different foods, an animal's changing nutritional state, or any other factors of interest. For example, Johnson *et al*. (2013) followed a female chacma baboon (*Papio hamadryas ursinus*) for 30 consecutive days and measured the protein and energy content of all food sources consumed by the individual, and then quantified her nutrient intake using the geometric method (Figure 3.1). They demonstrated that this individual was able to maintain a constant daily protein-intake, despite wide variation in the nutrient composition of the foods that were consumed (Johnson *et al*., 2013).

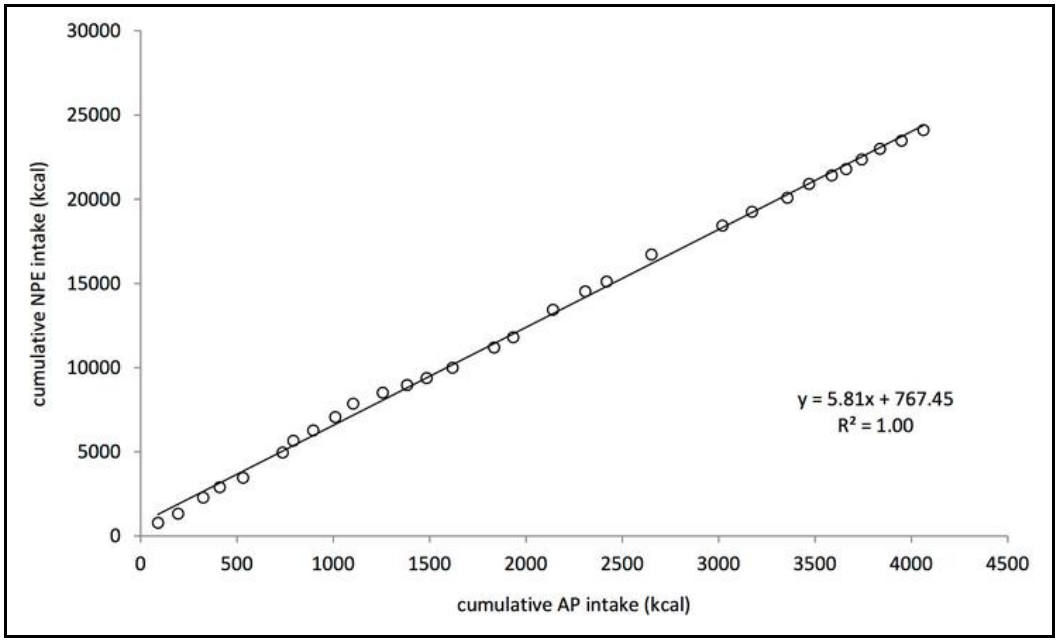

Figure 3.1. The cumulative intake of available protein (AP) and non-protein energy (NPE) by a female chacma baboon (*Papio hamadryas ursinus*) over 30 consecutive days, recorded using the geometric framework (Johnson *et al*., 2013).

The gravimetric method measures consumption, growth, and excretion, in order to establish how an organism performs on a variety of qualitatively different diets via a number of 'performance indices' (Waldbauer, 1968; Ahmad & Kamal, 2001), which include;

- Consumption rate (CR) = weight of food eaten/duration of the experiment (days)
- Growth rate (GR) = weight gain/duration of the experiment (days)
- Approximate digestibility (AD) = (weight of food eaten-weight of faeces)/weight of food eaten
- Efficiency of conversion of digested food into biomass (ECD) = weight gain/(weight of food eaten-faeces)
- Efficiency of conversion of ingested food into biomass (ECI) = weight gain/weight of food eaten

This study seeks to address the questions 1) what ratio of protein to carbohydrates do *H. thoracica* select in captivity? And 2) how efficiently do *H. thoracica* digest and metabolise protein and carbohydrates? Answering these questions will provide a better understanding of the nutritional requirements of these animals, which may direct their foraging choices in the wild. To determine the protein to carbohydrates nutritional target of *H. thoracica* (expressed from here on as 'P:C'), and reveal how efficiently these animals utilise the macronutrients protein and carbohydrates, a captive feeding experiment was performed. This experiment compared the consumption and performance of a choice group of *H. thoracica*, which were able to select their own diet from two incomplete food sources, to three non-choice groups of *H. thoracica* that were presented with set diets with P:C ratios of 20:80, 50:50, and 80:20.

3.2 Methods

3.2.1 Housing the Wētā

Wild *H. thoracica* were captured from the Waingaro Forest Reserve for the purpose of faecal fragment analysis (Chapter 2), 36 of which were still alive at the time this experiment was conducted. Seven additional wētā (three males and five females) were captured from the Mangaiti Gully in Hamilton to supplement their numbers, giving a total group size of 44, with 29 females (25 mature) and 15 males (12 mature). Each individual wētā was placed in a lidded, 2L plastic container. A square hole was cut in each lid, and covered over with 1 ml gauze mesh to allow air flow, and the containers were laid with moist paper towels as a

substrate and a source of water. A short length of plastic pipe was provided for each wētā to act as a daytime refuge, and the lid of a plastic Petri-dish was placed in one corner of each container. Each container was positioned randomly inside the animal containment facility of the University of Waikato to minimise the effects of any potential differences in light, temperature, or airflow. Although the room did have air conditioning, air-conditioning removes atmospheric humidity, and tree wētā require high atmospheric moisture to survive. Desiccation can rapidly kill tree wētā, and therefore, the temperature was allowed to fluctuate normally, without air conditioning. The experiment was conducted from 23.09.2013 through to 23.10. 2013. The groups were conditioned on their respective diets for one week and then starved for 48 hours before the experiment began in order to reduce the effect of residual gut contents on the wētās starting weights. The wētā were divided evenly and randomly between the four groups.

3.2.2 The Artificial Diets and Feeding Regime

Artificial food cakes were prepared following the methods of Cohen (2001), which used casein as the source of protein and sucrose as the source of carbohydrates. Multiple blocks of food were made in five different P:C ratios: 100:0, 0:100, 20:80, 50:50, and 80:20, and contained all essential nutrients. After preparation they were freeze-dried in a Labconco 'Freezone-6' lyophilising machine for three days, then sealed in plastic, zip-lock bags and kept in a freezer at -20ºC until needed.

At the start of day 1 of the trial, every wētā was weighed, and these readings were recorded as their starting weights. The wētā were then provided with fresh feed. Prior to feeding, the blocks of food were removed from the freezer, and 1cm^2 cubes (approximately) were cut from the blocks using a scalpel. The cubes were placed in a drying oven at 60ºC for three hours to remove any moisture they may have taken up from the air inside their bags over night. After re-drying the cubes were then weighed, and the weighed cubes were placed in individual, labelled plastic bags so the exact starting dry weight of each cube that was given to each wētā was known.

Each day, all of the *H. thoracica* in Group 1, the choice group, were given two food-cubes, one protein saturated with no carbohydrates and the other carbohydrate saturated with no protein, which they could choose between freely. The wētā in groups 2, 3, and 4 were each given a single cube with a non-varying

P:C ratio (Table 3.1). The cubes were placed in the Petri dishes to catch any pieces that broke off. The wētā were then left for 24 hours and the next morning all of the leftover food and all of the frass produced by each wētā was collected, labelled with the group and number of the wētā they belonged to, and then placed in a drying oven at 60ºC for three hours to desiccate. After drying, the leftover food and the frass were removed from the drying oven and the dry-weight of each was recorded. This process was repeated every day for 30 days. At the end of the 30 day period, all of the wētā were re-weighed, and the total dry weight of food eaten and frass produced by each individual was calculated.

3.2.3 Statistical Analysis

The data was analysed using Statistica 11.0. One way ANOVA was performed to determine whether there was any significant difference in the consumption of protein and carbohydrates by Group 1. The daily running totals of protein and carbohydrates consumed by this group were plotted geometrically to explore the consistency of daily P:C consumption, and regression analysis was performed to check the fit. One way ANOVA was used to test if P:C ratio had any significant influence on the total weight gain (TWG) or dry weight of food consumed (DWC) for each group, and Tukey's post-hoc comparison was used to determine which groups differed significantly from one another for each variable. The performance indices 'approximate digestibility' (AD) and 'efficiency of conversion of digested food into biomass' (ECD) were calculated for all of the wētā in each group, using the methods of Ahmad and Kamal (2001). One way ANOVA was used to determine if the protein to carbohydrate ratio had a significant effect on the digestibility or utilisation efficiency of the food, and Tukey's HSD post hoc comparison was used to determine which groups differed significantly.

Four wētā died before the experiment had ended, and six others rejected the artificial diet, even after the acclimation period. These individuals were excluded from the results, and the final group sizes were nine (Group 1), seven, (Group 2), nine (Group 3), and nine (Group 4) (Appendix 3.1). Because the sample size for each group was reletively small after accounting for individuals who either died, or refused the artificial diet, and the male to female ratio was heavily, male and female *H. thoracica* were grouped together for analysis, as any apparent difference between the males in any group, and the females, would be difficult to explore in any statistically robust manner.

3.3 Results

The choice group selected carbohydrate rich diet. The dry weight consumed was highest for groups 2 and 3, and the average weight gain was highest in group 4. Approximate digestibility decreased with increasing protein concentration of the diet, and was highest in group 1, and the efficiency of conversion of digested food in to biomass increased with increasing protein concentration of the diet, and was highest in group 4 (Table 3.1).

Table 3.1. The consumption (DWC) and weight gain (TWG), of *H. thoracica* fed on choice and non-choice diets with variable ratios of protein to carbohydrates (P:C), and the approximate digestibility (AD) and conversion-to-biomass efficiency (ECD) of those diets for each group.

	Group 1	Group 2	Group 3	Group 4
Number (N)	9	7	9	9
P:C	100:0 + 0:100	20:80	50:50	80:20
Average DWC (g)	0.4733 (28:71)	0.5423	0.6017	0.4837
Average TWG (g)	0.2079	0.2236	0.3470	0.5550
Average AD (%)	85.92	84.25	79.51	77.20
Average ECD (%)	44.66	45.95	72.90	94.70

3.3.1 Nutrient Balancing

There was inter-individual variation in both the ratios and quantity of food that were consumed by the wētā in the choice group, but each individual's daily intake was, more or less, stable for the duration of the experiment (Figure 3.2 A). The total dry weight (g) of protein consumed by these wētā over the 30 day period was 0.1336 g (Std.Err ± 0.059) and the total dry weight of carbohydrates consumed was 0.3397 g (Std.Err ± 0.061), which translates to a selected P:C ratio of 28:78. One way ANOVA revealed that the difference in consumption was significant ($F = 5.8310$; $p = 0.0281$). The mean consumption of protein and carbohydrates consumed each day by the group was consistent, with ($R^2 = 0.9863$) (Figure 3.2 B), and none of the wētā in this group consumed more protein than carbohydrates over the course of the trial (Figure 3.2 C). It appeared that the males in this group may have consumed more carbohydrates than the females, but with only two males to base this observation on, it would be difficult to support the results of any statistical comparison between the two sexes.

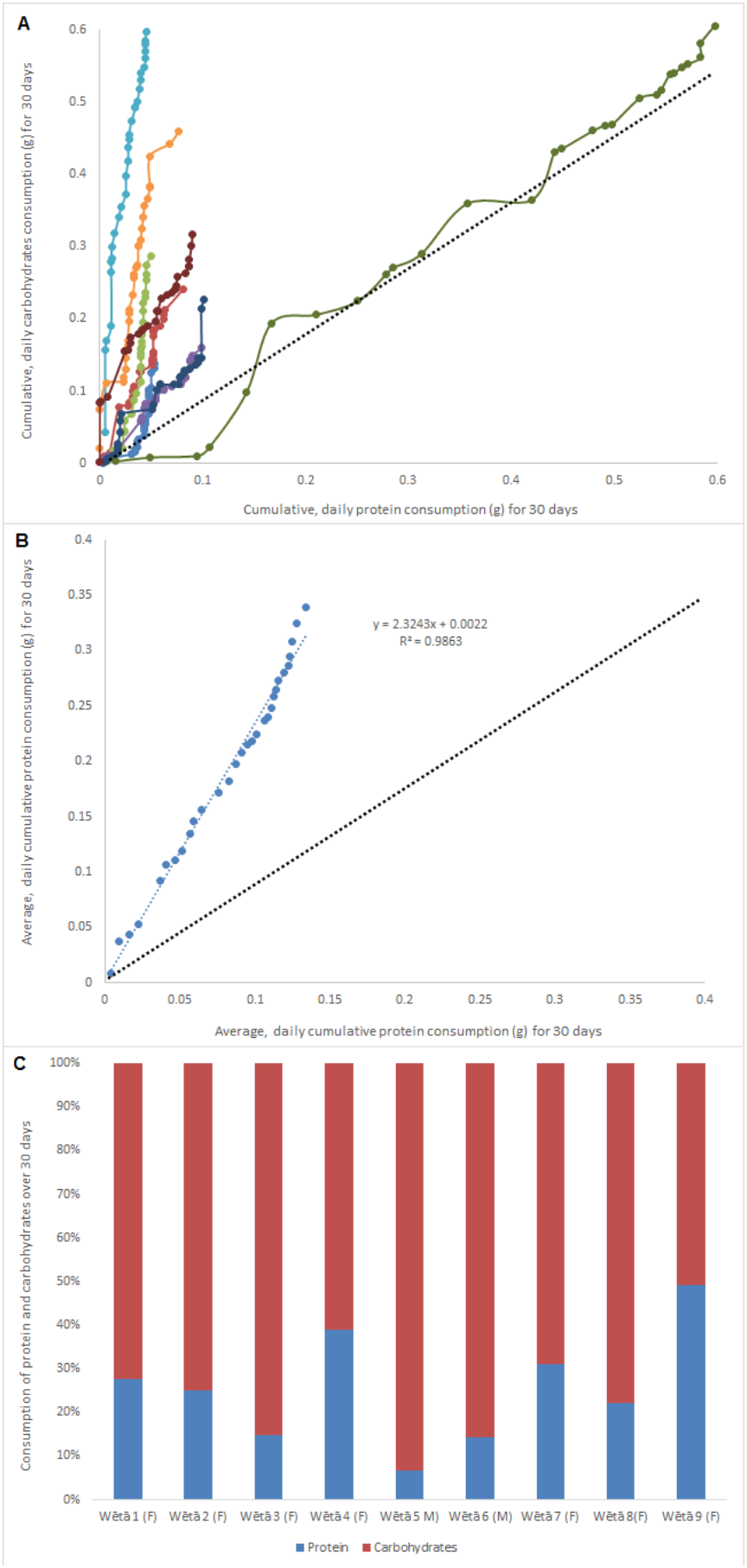

Figure 3.2. A) The cumulative consumption of protein and carbohydrates, B) the mean cumulative consumption, and C) the total P:C ratios consumed, by Group 1.

3.3.2 Total Weight Gain (TWG)

The TWG was lowest in Group 1 and highest in Group 4, with mean gains of 0.2079 g (Std.Err. ± 0.1076), 0.2236 g (Std.Err. ± 0.0495), 0.3470 g (Std.Err. ± 0.0907), and 0.3555 g (Std.Err. ± 0.0695), for groups 1, 2, 3, and 4 respectively (Figure 3.3 A). One way ANOVA detected no significant influence of P:C ratio on TWG ($p = 0.4487$; $F = 0.9083$).

3.3.3 Dry Weight of Food Consumed (DWC)

The mean DWC was highest in Group 3, and lowest in Group 1 and Group 4 (Figure 3.3 B). Mean DWC were 0.4733 g (Std.Err. ± 0.1059), 0.5423 g (Std.Err. ± 0.0712), 0.6017 g (Std.Err. ± 0.1048), and 0.4837 g (Std.Err. ± 0.0441), for groups 1, 2, 3, and 4 respectively (Figure 3.3 B). One way ANOVA detected no significant influence of P:C ratio on DWC ($p = 0.6959$; $F = 0.4840$).

3.3.4 Approximate Digestibility (AD)

Approximate digestibility was highest in the diets that had the highest concentrations of carbohydrates (Figure 3.3 C). The mean AD scores for groups 1, 2, 3, and 4 were 85.92 % (Std.Err. ± 2.3674), 84.25 % (Std.Err. ± 2.0444), 79.51 % (Std.Err. ± 1.9703), and 77.20 % (Std.Err. ± 1.7036) respectively (Figure 3.3 C). The choice group had the highest AD, followed by Group 2, and groups 3 and 4 had the lowest AD. One way ANOVA reveals that the P:C composition of the diet had a significant effect on digestibility ($F = 4.029$; $p = 0.016$), and Tukey's post hoc comparison revealed that there was a significant difference in AD between Group 1 and Group 4 ($p = 0.02$).

3.3.5 Efficiency of Conversion of Digested Food into Biomass (ECD)

The ECD was highest in the diets that had the highest concentrations of protein (Figure 3.3 D). The mean ECD scores for groups 1, 2, 3, and 4 were 44.66 % (Std.Err. ± 16.3896), 45.95 % (Std.Err. ± 6.1963), 72.90 % (Std.Err. ± 12.8351) and 94.70 % (Std.Err. ± 14.41) respectively (Figure 3.3 D). One way ANOVA reveals that the P:C composition of the diets had a significant effect on conversion efficiency ($F = 3.25061$; $p = 0.035$), and Tukey's post hoc comparison revealed that there was a significant difference in ECD between Group 1 and Group 4 ($p = 0.045$).

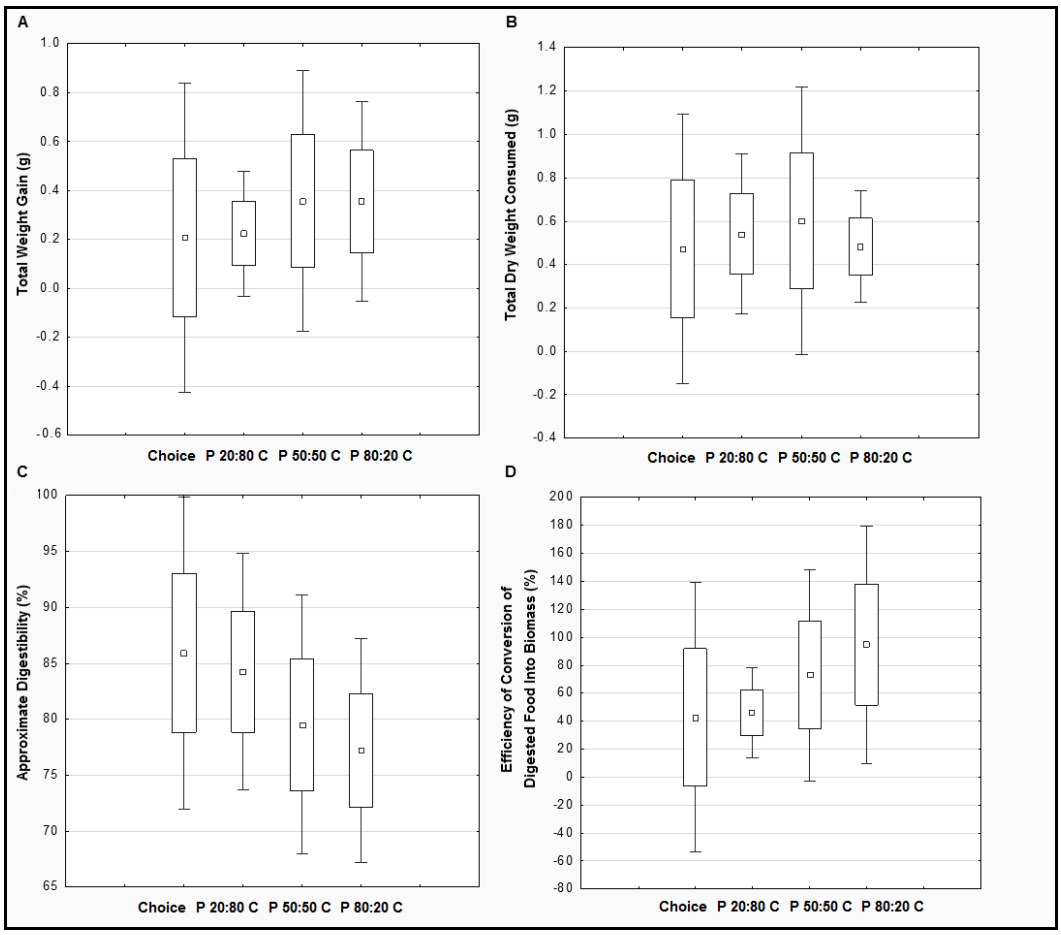

Figure 3.3. The A) total weight gain, and B) total dry weight of food consumed, by each group, and the C) approximate digestibility, and D) efficiency of conversion of digested food into biomass of each diet.

3.4 Discussion

This experiment sought to determine the nutritional target of *H. thoracica* as a ratio of protein to carbohydrates, and to demonstrate how effectively *H. thoracica* digest and metabolise these two macronutrients. The results determined that *H. thoracica* will preferentially select a carbohydrate rich diet, and metabolise protein with a high degree of efficiency.

3.4.1 Nutrient Balancing in *H. thoracica*

Griffin (2011) investigated the effect of increased protein consumption on the growth and fecundity of female *Hemideina crassidens*, and found that *H. crassidens* that were fed on a protein supplemented diet gained significantly more weight, and gained weight faster, than a group of *H. crassidens* that were fed on a low protein diet. Observing the high level of fat accumulation in the body cavity of the protein supplemented wētā, Griffin (2011) tentatively suggested that it may

be possible that *H. crassidens* have no ability to regulate their intake of protein. My results indicate that this is not the case, at least not for *H. thoracica*.

The *H. thoracica* in this study demonstrated an excellent ability to balance their consumption of the macronutrients protein and carbohydrates, and in captivity foraged to achieve a P:C ratio of 28:72. If *H. thoracica* were unable to regulate their protein consumption, or if a high level of fat accumulation were highly adaptive, then the choice group would have consumed more protein, and therefore *Hemideina thoracica* strongly regulate their consumption of protein. This has also been observed in the Wellington tree wētā *H. crassidens* (Wehi, *et al*., 2013), and other Orthoptera, such as the grasshopper *Locusta migratoria* (Simpson & Abisgold, 1985; Raubenheimer *et al*., 1992; Raubenheimer & Simpson, 1990, 2003). Although eight of the *H. thoracica* in the choice group consumed similar, carbohydrate rich diets, a single adult female from the Waingaro Forest Reserve consumed almost identical quantities of protein and carbohydrates (0.6 g and 0.62 g respectively). This female was fully mature, and all of the wētā in the choice group had been in captivity for five months by the time the experiment began, and kept separate from one another for that duration, so it is also unlikely that she was gestating eggs, so the reason why this wētā consumed more protein than the other eight wētā in the choice group is uncertain.

3.4.2 Weight Gain and Total Consumption

No significant difference was detected in either total weight gain or the dry weight of food consumed in this trial. Inter-individual variation was high in all four groups for both of these variables, resulting in overlapping confidence intervals, but even though significant differences were not detected between the groups, this does not necessarily mean there was no effect. Mean weight gain was lowest in the two groups that consumed low protein diets (groups 1 and 2) with mean gains of 0.2079 g and 0.2236 g, and highest in the two groups that consumed high protein diets (groups 3 and 4) with mean gains of 0.347 g and 0.3555 g. This could indicate that protein is positively correlated with the rate of weight gain in *H. thoracica*, but that the sample size may have been too small, and inter individual variation resulted in confidence limits that were too wide for the tests that were used to detect differences between groups. Although the non-choice groups with the highest protein concentrations accumulated more fat on average, as was observed by Griffin (2011), it is probable that was not due to an inability to

regulate their protein consumption, but rather a lack of opportunity to do so, after all, the choice group demonstrated strong regulation of their protein consumption. Almost any animal would gain weight if denied the opportunity for exercise, and provided with nothing to eat but high protein foods.

3.4.3 The Digestibility and Utilisation of Protein and Carbohydrates

The performance indices that were scored by the different groups, using the gravimetric method outlined in Ahmad & Kamal (2001), revealed that *H. thoracica* digests carbohydrates more efficiently than protein, but they convert protein into biomass with a much higher level of efficiency. The diet constructed by Group 1 (P 28:72 C) had the highest digestibility, with a mean AD of 85.92 %. Among the three non-choice diets, digestibility was negatively correlated with protein concentration, with mean AD scores for groups 2, 3, and 4 of 84.25 %, 79.51 %, and 77.20 respectively, and one way ANOVA revealed that the P:C ratio had a significant effect on conversion efficiency($F = 4.029$; $p = 0.016$).

On the other hand, the efficiency of conversion of digested food into biomass was positively correlated with protein concentration. Group 1, 2, 3, and 4 scored ECD values of 44.66 %, 45.95 %, 72.90 %, 94.69 %, and one way ANOVA revealed that the P:C ratio had a significant effect on the conversion efficiency of the diets ($F = 3.25061$; $p = 0.035$). This could mean that protein is a limiting resource for *H. thoracica* in the wild, as they appear to have evolved to utilise it as efficiently as possible when it is available. Being able to convert protein into body mass with an extremely high level of efficiency could have multiple benefits for tree wētā living in the wild. Protein consumption has been shown to accelerate the growth rate of *Hemideina crassidens*, meaning that exploiting protein efficiently could enable them to reach sexual maturity more rapidly (Griffin, 2011). Converting protein into mass with a high level of efficiency would also enable wild *H. thoracica* to rapidly build up their energy reserves when protein rich food was available, enabling them to forage less frequently, and reduce the amount of time that they are exposed to the cold, desiccation stress, and the vertebrate animals that eat tree wētā.

3.4.4 Relating these Results to the Diet of *H. thoracica* in the Wild

In Chapter Two, analysing the food fragments in the frass of wild *H. thoracica* showed that the diet of that population was dominated by leaves, but fragments

from other invertebrates were also common and formed a smaller component of the overall diet. If these individuals were feeding optimally for this species, and this composition reflected an optimal, natural diet for *H. thoracica*, then we would expect that *H. thoracica*, provided with the opportunity, will select a diet that is rich in carbohydrates. When given the opportunity to select their own diet in captivity, the choice group of *H. thoracica* consumed a diet of 28 % protein and 72 % carbohydrates, indicating that their natural diet is mostly composed of plant materials (carbohydrate heavy foods). The results of this experiment therefore indicate that the composition of the diet that was determined for *H. thoracica* from the Waingaro Forest Reserve was probably representative of an optimal diet for this species.

3.4.5 Limitations

The major limitation of this study was the skewed female to male sex ratio of the wētā. The *H thoracia* that had been captured from the Waingaro Forest Reserve for faecal fragment analysis, in March and April, had originally been in a 1:1 ratio, but by the time this experiment began in September, more males than females had died, plus several more males rejected the artificial diet and so were excluded from the results. I attempted to suppliment the numbers with *H. thoracica* captured in Hamilton, but the majority of the captured wētā were female also. Having only 2-4 male *H. thoracica* in each group made it unrealistic to statiscally compare the two sexes in any group. One way ANOVA was performed to compare the DWC, TWG, AD, and ECD, of males and females in each group, and no differences were discovered in any variable, in any group, except for the ECD in group 3, where the females appeared to have significantly greater conversion efficiency than the males (results not shown). However, there were only two males in this group, compared to seven females, and the sexes were not found to differ in this variable in any other group. Also, the two males in the choice group appeared to have consumed more carbohydrates than the females in that same group, but whether this is typical or not, could not be determined in this study. Fragment analysis of the diet of wild *H. thoracica* revealed that there was no difference in the range or composition of the diet of either sex (Chapter 2), however, it may be possible that this was because male *H. thoracica* do not have as much opportunity to feed differently in the wild, only having access to the same foods as the females, and in captivity they may still self-select a different

diet, and perform differently than females. A follow up nutrient balacing study needs to be performed, using male and female wētā in a more comparable ratio.

3.4.6 A Personal Observation

While filming a male wētā in the P 80:20 C group feeding, I watched while he gnawed on his food cube, off of which a number of crumbs and smaller chunks had broken away. While feeding, one of his palps touched one of the smaller fragments, and he rapidly discarded the large cube to eat the smaller fragments. It makes sense that *H. thorac*ica may elect to consume smaller food items over larger ones, as a lower handling time could mean higher consumption, and a greater energy gain per unit of time spent foraging. This should be explored with a study that measures the consumption and performance of groups of *H. thoracica* (or another invertebrate generalist) on intact and fractured diets.

3.5 Conclusions

The tree wētā *H. thoracica* balances its consumption of protein and carbohydrates, and selects a carbohydrate rich diet. They also digest carbohydrates more easily than protein. These combined facts support the results of the fragment analysis I performed on the frass of wild *H. thoracica*, which found that their natural diet in the wild was mostly composed of leaves, and that they feed selectively, suggesting that this composition represents optimal foraging for this species. Although protein is a smaller component of their diet, it may be limiting to *H. thoracica* in the wild, because they have evolved to exploit it by converting it into body fat with a high level of efficiency when it is available.

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4 Chapter 4: The Tree Wētā *Hemideina thoracica* does not feed on Fruit in a Manner that Could Facilitate Seed Dispersal.

4.1 Introduction

Mutualism is defined as '*a symbiotic relationship in which both partners benefit'* (Campbell *et al*., 1994, p 811). Mutualistic interactions may frequently develop between a fruiting plant and a frugivorous animal, in which the animal eats the fruit produced by the plant, and then disperses the seeds in its faeces (Howe & Smallwood, 1982; Ruxton & Schaeffer, 2012). Animals that successfully deposit more seeds than they destroy, or that provide the surviving seeds with some benefit that outweighs the cost of the seeds that were destroyed, are referred to as seed dispersers (Schupp, 1993). On the other hand, seed predators destroy the seeds that they consume, and the plant derives no benefit from the interaction and may even suffer a net loss in reproductive fitness as a result (Hulme & Benkman, 2002). These interactions play an important role in determining the composition and spatial structure of plant communities (Godinez-Alvarez,. *et al*. 2002; Levin,. *et al*. 2003; Levine & Murrell, 2003; Spiegel & Nathan, 2007). Seed dispersal interactions between frugivores and fruiting plants have important implications for the conservation and restoration of forest ecosystems, as they affect the number of seeds that are successfully recruited, which in turn alters the successional development of the forest, and the climax state of the ecosystem.

Tree wētā are large-bodied, nocturnal, flightless insects from the order Orthoptera, and are endemic to New Zealand. They are known to consume fleshy fruits and it has been demonstrated that some species of tree wētā are capable of passing intact seeds through their digestive tracts (Duthie *et al*., 2006; Morgan-Richards *et al*., 2008), which is unique among insects (Larsen & Burns, 2012) and unusual considering the digestive physiology of the animal. Tree wētā possess highly versatile mouthparts, capable of both slicing and crushing food, and a complex grinding organ called a proventriculus. This organ takes up much of the inside of the thorax, and contains multiple parallel rows of hardened teeth that project into the lumen (Maskell, 1927). Between the slicing and crushing actions

of their mouthparts, and the additional grinding that occurs in the proventriculus, the likelihood of a seed being consumed whole, and then passing through the foregut intact, is probably low (Maskell, 1927). The fact that tree wētā do have the potential to pass some seeds through their digestive tract intact has sparked an ongoing debate about whether or not this trait facilitates a mutualistic, co-evolutionary interaction, whereby tree wētā disperse the seeds of native fruit-bearing plants (Duthie *et al*., 2006; Morgan-Richards *et al*., 2008; Fadzly & Burns, 2010; Wyman *et al*., 2010; Larsen & Burns, 2012).

Larsen and Burns (2012) found that the alpine scree wētā (*Deinacrida connectens*) is capable of swallowing the seeds of mountain snowberries (*Gaultheria depressa*), and passing them through their digestive tracts intact with varying degrees of effectiveness. They found that seed dispersal effectiveness was strongly associated with body size, and smaller weta consumed few *G. depressa* seeds and acted primarily as seed predators, whereas the largest wētā consumed and dispersed a large number of seeds and appeared to be capable of transporting seeds over large distances (Larsen & Burns, 2012). Likewise, body size has also been demonstrated to be positively correlated with the successful passage of *F. excorticata* seeds through the digestive tract of the Wellington tree wētā, *H. crassidens* (King *et al*., 2011).This may indicate that some tree wētā species shift from being seed predators as juveniles, to seed dispersers as they mature and increase in size (Larsen & Burns, 2012). Duthie *et al* (2006) investigated the post ingestive fate of seeds consumed by the Wellington tree wētā *H. crassidens*. They determined that *H. crassidens* were capable of passing the seeds of *Fuchsia excorticata*, *Pratia physaloides*, and *Gaultheria depressa* intact through their digestive tracts, and that the germination rates of such seeds were slightly higher (10 %) for *F. excorticata* and *P. physaloides*, than for seeds that were manually extracted from the fruit. However, they also found that 78 % of the seeds that were consumed were destroyed, and so, rather than determining whether *H. crassidens* can pass any viable seeds through their digestive tract, it may have been more useful for them to determine whether or not the benefit gained by the surviving seeds outweighed the cost of the seeds that were destroyed.

It has been well-document that many fruiting species have evolved conspicuously coloured fruit, in order to attract the attention of dispersers (Ridley, 1930; Van Der Pijl, 1982; Schaeffer *et al*., 2006), although it is unclear how prevalent this is in New Zealand. Electroretinogram studies performed on

Hemideina and *Deinacrida* wētā show that their peak visual sensitivities range from 440 to 530 nm, which correspond to the blue and green wavelengths (Field, 2001). A high percentage (21.2 %) of the fleshy-fruited flora of New Zealand have white or blue fruit (Lee *et al*., 1988, 1990, 1994, 2006; Wilson *et al*., 1989; Lord *et al*., 2002), and Fadzly & Burns (2010) demonstrated that *H. crassidens* preferentially selected naturally blue *Coprosma acerosa* fruit, as well as blue-dyed fruit, over fruits dyed red ($p < 0.01$). They suggest that this could indicate that New Zealand angiosperms have evolved pale-coloured fruit in order to advertise to foraging wētā, for dispersal purposes.

Morgan-Richards *et al*., (2008) have suggested that while the aforementioned studies provide grounds for debate, the existence of a mutualistic interaction between the fruiting plants of New Zealand and tree wētā is doubtful, as mutualism would only occur if the benefit gained by the plant from having its seeds consumed outweighed the cost of seed predation. Wyman *et al*. (2010) pointed out that the modest benefit these plants received in the form of improved seed germination could easily be outweighed by the loss of seeds to predation, resulting in a net fitness decrease for the plant, and this would mean that tree weta are seed predators, not seed dispersers, even if they sometimes pass viable seeds. They further suggested that tree wētā could have a negative effect on plant fitness if they deposit the seeds they consume closer to the parent plant than if the seeds had dispersed by some other means, such as water or gravity (Wyman *et al*., 2010). This experiment investigated whether or not the Auckland tree wētā *H. thoracica* consume fruit in a manner that could potentially facilitate successful seed dispersal for plants in the wild.

4.2 Methods

Adult male (N = 15) and adult female (N = 25) *H. thoracica* that had been captured earlier, between March and April, from a privately owned section of the Waingaro Forest Reserve, were used in the experiment. Before the experiment began, all of the wētā were weighed (g), and the length and width of the head of each of the wētā was measured (Appendix 4.1), so that weight and size could be compared against the number of seeds passed intact (if successful seed passage occurred). Each individual wētā was placed in a lidded, 2L plastic container. A square hole was cut in each lid, and covered over with 1 ml gauze mesh to allow

air flow, moist paper towels were laid down in containers as a source of water, and a short length of plastic pipe was provided for each wētā to act as a daytime refuge. Each container was positioned randomly inside the animal containment facility of the University of Waikato to minimise the effects of any potential differences in light, temperature or airflow. The room had air conditioning, but air-conditioning removes atmospheric humidity, and tree wētā require high atmospheric moisture to survive. Desiccation can rapidly kill tree wētā, and therefore, the temperature was allowed to fluctuate normally, without air conditioning. The wētā were kept like this for two months from March and April when they were captured, till June when the experiment began, and during that time, they were maintained on a constant diet of leaves from *Coprosma repens* and *Melicytus ramiflorus*. Twice a week they were provided with *Coprosma repens* berries, or small cubes of fresh apple, and once per week they were each given a live mealworm for protein.

Three different species of native fruits were used in the experiment, *Coprosma repens* (Figure 4.2 A), *Cordyline australis* (Figure 4.2 B), and *Fuchsia procumbens* (Figure 4.2 C). Fruit were collected in late June from plants on the University of Waikato campus grounds, and measurements were taken of 12 randomly selected fruit from each species. The seeds were extracted, counted, and measured, to estimate their length and width, and the mean number of seeds per fruit was calculated (Appendix 4.2), in order to determine the average number of consumed seeds of any fruit that were successfully passed intact (if any).

The wētā were starved for 48 hours before the trial began in order to encourage them to eat. In the first round of the experiment, the wētā were presented with the drupes of *C. repens*. Each subject was provided with three berries, scattered randomly around the inside of their enclosure. After 24 hours I recorded which wētā had consumed the pericarp (fleshy part) of the fruit, and whether or not any seeds had been eaten either partially or completely. All of the faecal pellets (called 'frass') were collected, bagged, and labelled, and the wētā were starved for another 48 hrs in order to keep them hungry before the second round. In the second round of the experiment, each wētā was provided with three *C. australis* berries, and the process was repeated. Finally, in the third round of the experiment, I presented each wētā with *F. procumbens*. This time, each wētā was presented with a quarter of a berry, rather than three whole ones, as *F. procumbens* is a naturally uncommon plant and 40 ripe berries could not be

located. I acquired ten *F. procumbens* berries, carefully cut each berry into four quarters, each containing one whole locule, and each wētā was then presented with one locule. 40 wētā were used in the first two rounds (*C. repens* and *C. australis*), but during the 48 hour starvation period after the *C. australis* round of the experiment, two wētā passed away. Because of this, 38 wētā were used in the third round of the experiment (*F. procumbens*).

To analyse the frass, each pellet was placed in a mortar with 5 ml of distilled water, and then broken apart gently into small pieces using a metal probe. The solution was manually stirred vigorously to further degrade the matrix of digested materials that the seed fragments were lodged inside. The solution was then poured out into a paper coffee filter, with the dissolved frass and seed fragments. The contents were examined on the filter under an Olympus SZH10 stereo-microscope, to attempt to find any complete seeds that may have passed through the alimentary canal intact.

4.3 Results

In all three rounds of the experiment, the wētā consumed the pericarp of the fruit, without consuming any of the seeds, more often than they consumed both the pericarp and the seeds together. Unconsumed seeds were typically left undamaged, but in no round of the experiment did any consumed seeds successfully pass intact through the digestive tracts of the wētā intact. Males also consumed more fruit than females in all three rounds of feeding (Figure 4.1). No statistical comparison of any potential relationship between the size/weight of the *H. thoracica* and the percentage of seeds successfully passed could be performed since no seeds actually survived gut passage.

In the first round, 44 % of the females consumed at least one of the *C. repens* drupes that they were provided, and 8 % consumed two. 93.33 % of the males consumed at least one drupe, and 26 % of the males consumed two. All of the seeds were left intact with no signs of damage from feeding (Figure 4.2 D1).

In the second round, 60 % of the females consumed at least one of the *C. australis* berries provided, 16 % ate one berry, 8 % ate two berries, and 36 % ate all three. On the other hand 75.55 % of the males consumed at least one berry, 20 % consumed two berries, and 11.11 % ate all three. One male and two females

ate the seeds from one berry, and one female wētā ate all of the seeds from all three berries.

In round three, the percentage of males that ate the fruit they were provided was higher than the percentage of females. 40 % of the females consumed ate at least part of the *F. procumbens* locule they were provided, and 12 % ate the whole locule and all of the seeds. On the other hand 61.53 % of the males consumed at least some of the *F. procumbens* locule, 50 % of whom consumed the entire locule and all of the seeds therein. Wētā that consumed the entire locule often produced so much seed material in their frass that seed fragments were visible to the naked eye, but no intact seeds were observed in the frass (Figure 4.2 D2).

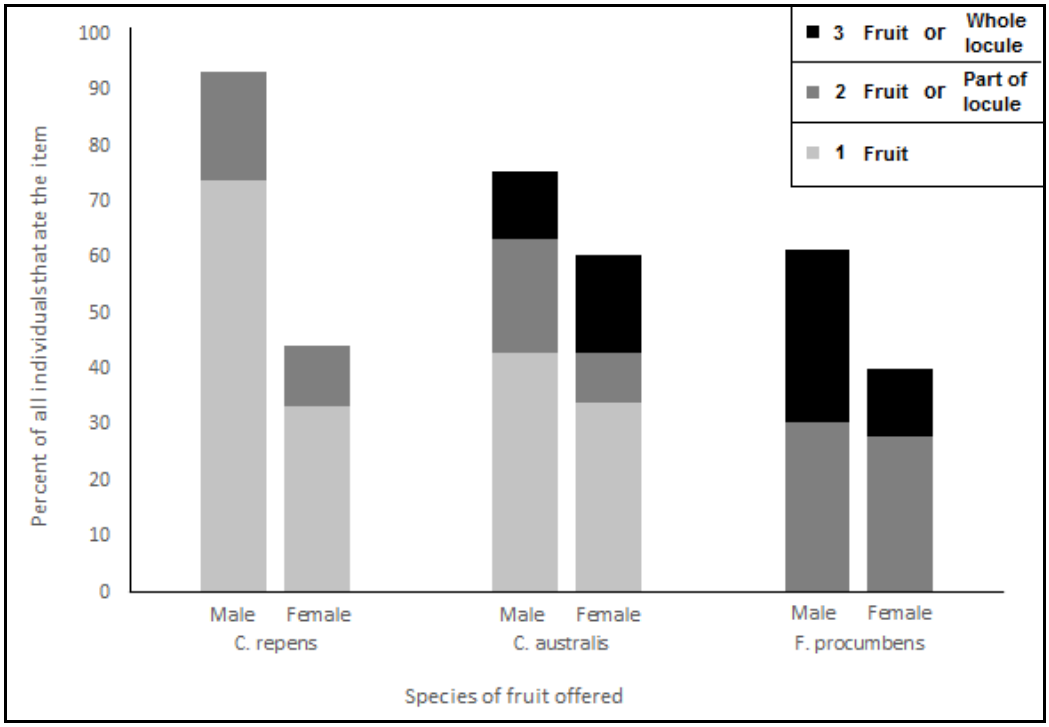

Figure 4.1. The proportion of male and female *H. thoracica* that consumed 1, 2, or 3 fruits of *C. repens* and *C. australis*, and the proportion that ate either part, or all, of a *F. procumbens* locule.

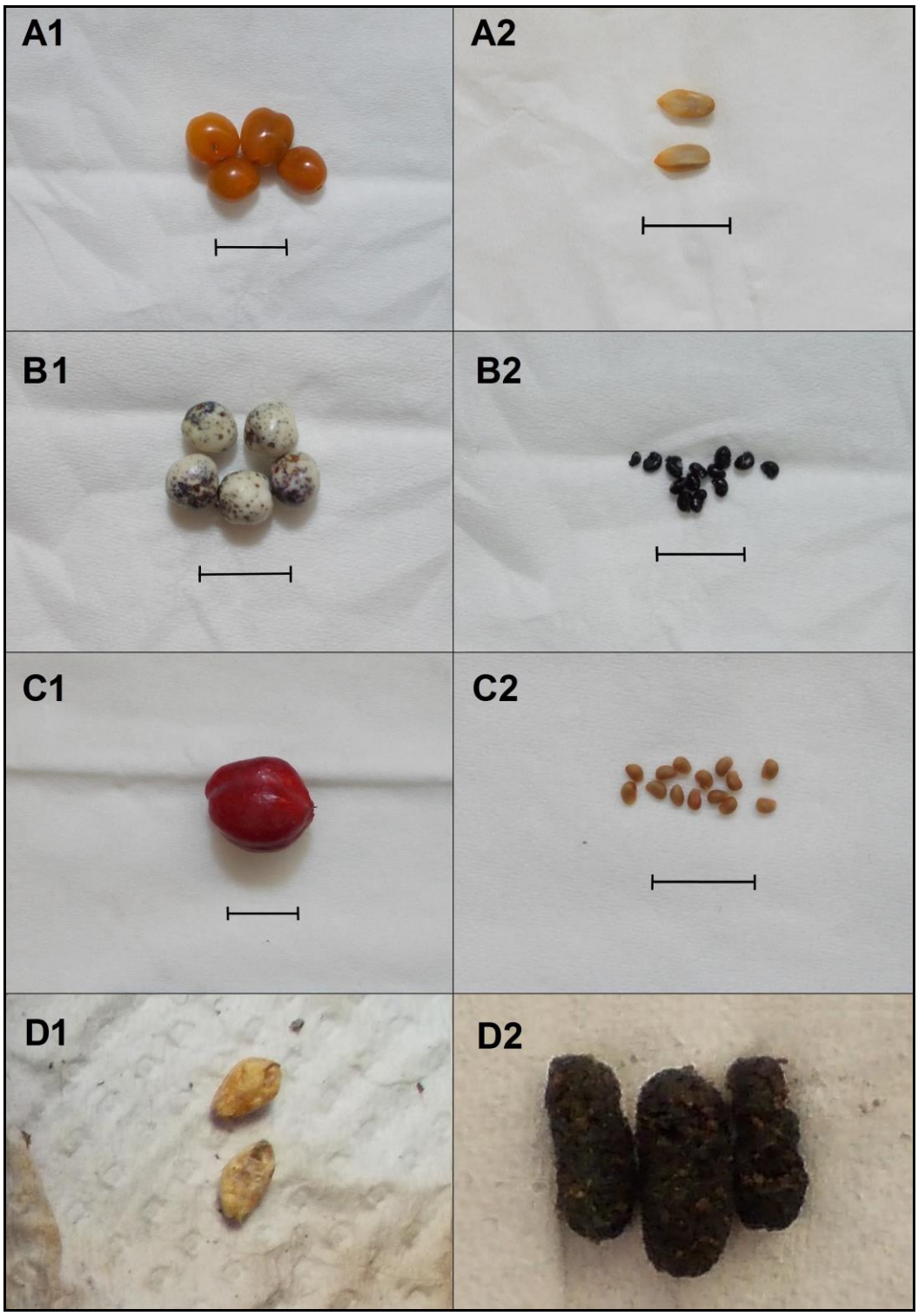

Figure 4.2. A) ***Coprosma repens*** **(1) drupes and (2) both seeds extracted from a single drupe. B)** ***Cordyline australis*** **(1) berries and (2) all seeds extracted from a single berry. C)** ***Fuchsia procumbens*** **(1) berry and (2) all seeds extracted from a single locule. D1)** ***Coprosma repens*** **seeds after the pericarp has been stripped away by** ***H. thoracica*****. D2) Visible seed fragments from** ***F. procumbens*****, still lodged in the frass after gut passage. All scale bars are 1 cm. All photos by Author (2013).**

4.4 Discussion

The *H. thoracica* readily consumed the fruit of all three plant species that were offered to them in this trial. *Coprosma repens* drupes contain the largest seeds out of the three different fruiting species used in this trial, and 44 % of the females and 93 % of the male wētā consumed some, or all, of the pericarp of at least one drupe, but none of them ate the seeds, all of which were left completely intact. 60 % of all female wētā and 75.5 % of the males consumed the pericarp of at least one of the *C. australis* berries, and three of those wētā consumed the seeds of one or more berries, and although the seeds of *C. australis* are considerably smaller and more numerous than those of *C. repens*, none of the *C. australis* seeds were passed intact. The berries of *F. procumbens* have, by far, the greatest number of seeds and the smallest seeds of all the plants in this trial, and 12 % of the females (3 wētā in total) and 30.77 % of the males (four wētā in total) consumed the entire locule they were given as well as all of the seeds inside. Despite this, not one single intact seed was found in any of the frass, which was typically full of ground-up and broken *F. procumbens* seed fragments.

The male *H. thoracica* appeared to eat more fruit than the females. More of the male *H. thoracica* ate the fruit that were offered to them in each round of the trial, and more of the males consumed two or three out of the three fruit they were given in the first two rounds of the trial, rather than just one. More of the males also consumed the entire *F. procumbens* locule they were give, rather than just part of it. Why the males in this study appeared to consume more fruit than the females is uncertain. Fragment analysis of these same *H. thoracica* in their natural habitat (the Waingaro Forest Reserve) showed no difference in fruit and seed consumption between males and females, except in a single location where the males actually did produce more fruit and seed fragments than the females from that same location (Chapter 2). This matter warrants follow up study.

4.4.1 Disperser Effectiveness is Dependant on the Quantity of Seeds Moved, and the Quality of Seed Treatment and Deposition

Disperser effectiveness is the contribution a disperser makes to the future reproduction of a plant, and depends on the quantity of seeds they successfully disperse and the quality of subsequent dispersal (Herrera & Jordano 1981; Schupp, 1993), and different groups of animals differ in their effectiveness as dispersers (McKey 1975; Howe & Estabrook 1977; Wheelwright & Orians, 1982; Levey

1987). The quantity of seeds moved by *H. thoracica* would be low. Faecal fragment analysis of the frass of wild *H. thoracica* from the Waingaro Forest Reserve (Chapter 2), revealed that their natural diet is primarily composed of leafy materials, with fruit and fruit-like structures forming a smaller component of the overall diet. If this is accurate, then they are not obligate frugivores, and thus the likelihood of them even consuming fruit or seeds in any bout of foraging would be lower than for a more highly frugivorous animal. Wyman *et al*., (2010) found that, when captive *H. crassidens* were given a choice of a *Melicytus ramiflorus* leaf or a *Fuchsia excorticata* fruit, 41% ate only the leaf, whereas only 14% ate only the fruit, and in no observation was the entire fruit eaten. This adds additional support to the theory that *Hemideina* in general are not highly dependent on fruit as a food source, and as such probably do not move a great enough quantity of seeds to be considered seed disperser mutualists.

Seed dispersal quality is a combination of the treatment the seed receives in the mouth and in the gut, and the suitability of the site where the seed is eventually deposited (Howe, 1986; Schupp, 1993). The tree weta used in these trials tended to eat around the seeds of *C. repens* and *C. australis*, consuming only the pericarp, and captive *H. thoracica* will also consume kawakawa (*Macropiper excelsum*) fruit, which have many small seeds embedded throughout the pericarp, without consuming the seeds (MB pers. obs.). Seed treatment in the mouth is therefore likely to be minimal for *H. thoracica*.

Tree wētā inhabit wood holes referred to 'galleries', from which they emerge at night to feed before returning again, and Kelly (2006) estimated the maximum nightly movement rate of *H. crassidens* to be 12.07 ± 1.57 m/night^{-1}. This suggests that tree wētā feed in a limited radius surrounding their gallery, within which they will deposit most of their frass. Wyman *et al* (2010) observed that when *H. crassidens* consumed *F. excorticata* fruit, 63.5 % of the faecal pellets that were produced afterwards were deposited within the same 10 × 10 cm^2 quadrat as the wētās gallery. Therefore, if tree wētā do not travel far in any single night, and deposit the majority of the frass they produce close to their gallery entrance, then there is a high likelihood that any seed that did pass through their digestive tract intact would be deposited directly under, or near, the parent tree. Proximity to parent plants frequently has a negative impact on seedling survival and recruitment, due to seed predators, pathogens, and other natural enemies that concentrate around parent trees (Janzen, 1970; Levin *et al*., 2003). Empirical

studies have shown that most plant species suffer increased mortality in areas where the densities of conspecific seeds, seedlings, or adults are high (Harms *et al*., 2000; Levin *et al*., 2003), and Howe (1993) showed that the survival of *Virola nobilis* (Myristicaceae) seedlings increased as a function of distance from their parent trees ($p < 0.001$). If tree wētā deposit intact seeds close to the parent tree, then those seeds may also suffer a reduced likelihood of post-germination survival compared to seeds dispersed by more-mobile vectors. Tree wētā seed dispersal is probably short-ranged, and therefore there is a high probability that they will deposit the few seeds that they consume, and which survive gut-passage, in close proximity to the plant that produced those seeds.

4.4.2 Seed Dispersers Should Destroy Few of the Seeds they Ingest, or Provide a Substantial Benefit to the Seeds that Survive.

Frugivorous animals that are usually considered to be successful seed dispersers seldom damage seeds during gut passage (Schupp, 1993). Based on this definition, *H. thoracica* and other tree wētā species could not be considered seed dispersers, as the majority of seeds that they do ingest are destroyed. In this study all of the seeds consumed by the *H. thoracica*, even very small seeds, were destroyed by the digestive process. This is not surprising considering the series of mechanical and chemical digestive processes that comprise a tree wētās alimentary canal (Maskell, 1927). Mirams (1957) studied the factors that affect the recruitment of kauri trees (*Agathis australis*) in the wild, and observed that wild *H. thoracica* consume the seeds of kauri (*Agathis australis*) on the forest floor, and that all of the seeds that are consumed in this manner are destroyed in the process. They observed that when *H. thoracica* feed on *A. australis* seeds, they crushed the seed coat with their jaws, in order to consume the oily contents. Fadzly & Burns (2010) found that 84 % of *Coprosma acerosa* seeds consumed by *H. crassidens* were either destroyed, or fail to germinate after they complete gut-passage, and Wyman *et al*., (2011) found that when *H. crassidens* consume *F. excorticata* berries, 78 % of the consumed seeds are destroyed.

The survivorship of seeds consumed by tree wētā is extremely low compared to seed survival rates of almost 100% in some frugivorous birds (Fukui 1995; Yagihashi *et al*,. 1998). While the survivorship of seeds consumed by wētā is extremely low, Duthie *et al* (2006) found that passage through the gut of *H. crassidens* actually resulted in a 10 % increase in the germination rate of ingested

seeds that did survive. In their study 78 % of the ingested seeds were destroyed, but the surviving seeds had a 95 % germination success rate, compared to a germination success rate of 85 % for manually extracted seeds, causing them to conclude that wētā form mutualistic partnerships with fleshy-fruited plants (Duthie *et al.*, 2006). However, if the proportion of manually extracted seeds that germinated in their study was 85 %, but the proportion of consumed seeds that successfully germinated was only 21 % (0.22 seed survivorship × 0.95 germination success), then a 10 % increase in germination quality is not high enough to compensate for the quantity of seeds that were destroyed. Additionally, if a plant is already seed limited in its recruitment, then the destruction of a large number of seeds by foraging wētā could have serious negative fitness implications for the plant. Bell (2010) demonstrated that recruitment of the tree fuchsia *F. excorticata* is both seed and herbivore limited. Therefore, if approximately 80 % of *F. excorticata* seeds that are consumed by tree wētā are destroyed, then the interaction is actually antagonistic towards the plant.

4.4.3 Tree Wētā May Still Influence Plant Community Composition Via Other Interactions.

While the available evidence indicates that tree wētā probably cannot be considered seed dispersers, they may still have a significant influence on the structure of their ecosystems via seed predation. Defaunation syndrome occurs when the loss of browsing mammals from the forest causes a huge increase in the number of seedlings on the forest floor (Dirzo & Miranda, 1991; Howe & Miriti, 2004). This results in a marked decrease in diversity over time because, without browsers to thin their seeds and saplings, more aggressive species are less restrained in their recruitment (Howe *et al.*, 2004). When I performed a fragment analysis on the frass of wild *H. thoracica* captured from the Waingaro Forest Reserve (Chapter 2), the results led to the conclusion that *H. thoracica* probably do most of their foraging on the forest floor. If this theory is correct, and *H. thoracica* actually forage primarily on the forest floor, then the berries and seeds they encounter would be those that dropped to the forest floor, directly under, or near, the parent plants. By preying on fallen berries, and destroying the seeds of the most abundant fruits, tree wētā could promote species diversity by preventing highly fecund plants from dominating the plot.

4.5 Conclusions

The question of whether or not tree wētā are legitimate seed dispersers cannot be answered by observations of the animals alone, without examining their effects on seed and seedling survival, and recruitment. The question is more complex than simply whether or not they can successfully pass seeds intact. The percentage of ingested seeds that pass intact, and the eventual fate of wētā dispersed seeds, needs to be compared to those of seeds dispersed by other means. If the quantity of seeds moved are too low to outweigh the cost of those that are destroyed, then tree wētā cannot be considered legitimate dispersers, and if seed deposition by tree wētā has a lower range than other dispersal mechanisms, or results in seeds being deposited in an unsuitable location, then any tree wētā dispersed seeds that do become saplings may still experience increased mortality.

The results of this experiment indicate that *H. thoracica* cannot be considered seed dispersers, as they often ignore seeds completely during feeding, and when they do consume seeds, they tend to destroy more than could be made up for by any increase in germination that may be gained by any survivors. If this is how *H. thoracica* eat fruit in the wild, then the seeds will either be left laying where the fruit was consumed, or the seeds will be consumed, but destroyed in the process, and therefore the plants gain no reproductive benefit via the interaction. There does not appear to be sufficient grounds at this point in time to suggest that the fruiting plants of New Zealand, and *Hemideina* wētā as a group, have evolved any mutualistic partnerships. These interactions may even result in a net decrease in reproductive success for the plant due to the loss of propagules to seed predation, making the relationship between *H. thoracica* and fleshy-fruiting plants an antagonistic one. It is still possible that seed predation by tree wētā fulfils an important ecological role, and has a net benefit to the community as a whole. The predation of fallen seeds by ground-foraging wētā could facilitate species diversity by preventing highly fecund plants from dominating the plot entirely. This possibility warrants investigation.

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5 Chapter 5: Observations and Recommendations for Follow-Up Studies

5.1 The Utilisation of (*Ligustrum sinense*) by *Hemideina thoracica* and *Aenetus Virescens*

While capturing *H. thoracica* from the Waingaro Forest Reseve, I noticed that the majority of the tree wētā captured on the terrace had been living in deep, vertical holes bored into the stems of privet (*L. sinense*), and 13 of the 18 wētā captured at this location were extracted from privet. I came to recognise distinct, entry holes in the privet, and I extracted live pupae of the puriri moth *Aenetus virescens* from several identical holes. I also found some exoskeletal fragments belonging to a puriri moth pupa in a privet-hole occupied by a male tree wētā (Figure 5.1). These tunnels were reasonably large, nearly two centimetres in diameter, and up to eight inches long, and are therefore big enough to accommodate multiple wētā, which I did observe in some instances. Native trees that were common in the same location (including *Coprosma*, *Pennantia*, and *Melicytus*) showed very little evidence of *A. virescens* bore tunnels, and it seemed that *A. virescens* caterpillars may select *Ligustrum* preferentially. While privet is considered a problematic invasive species, it is interesting to note that puriri moth caterpillars use it to develop, and may even prefer it over native species, and when the adult moths have vacated the bore holes, tree wētā use them as a daytime refuge. Realistically, the vegetation of New Zealand has been so drastically altered by human interference that many invasive plant species cannot be removed, and are no longer invaders, so much as permanent components. Because of this, it may provide valuable information on the realised niches of some of these species to start investigating them as realised components of their adoptive habitats, and begin searching for mutual interactions that might be developing between them, and native plants and animals.

Figure 5.1. A male *H. thoracica* inside the stem of a privet *L. sinense*. The tunnel was originally bored by the caterpillar of the puriri moth *A. virescens*. The black hemisphere, visible near the bottom/centre of the image, is an eye-lens from the pupae that bored the tunnel. Photo by author (2013).

5.2 Do the Male Tree Wētā Consume More Carbohydrates than the Females?

The fragment analysis portion of this study (Chapter 2) revealed that there was no significant difference in the diversity, or composition of the diets that were eaten in the wild by male and female *H. thoracica*, but in the nutrient balancing study (Chapter 3) the two male tree wētā in the choice group appeared to consume even more carbohydrates than the females. Males in the seed-eating trial (Chapter 4) also appeared to eat more fruit than the females did in all three rounds of the trial. It may be that in the wild, male *H. thoracica* have less opportunity to feed differently to the females, as they have access to more or less the same food items, but when they have the opportunity (in captivity) it is possible that they might selecte a different optimal-diet P:C ratio than that of the females. Comparing the consumption of protein and carbohydrates in the choice group, in this study, was difficult to do due to the skewed ratio of females to males. I determined that *H. thoracica* have a strong ability to nutrient balance, and select a carbohydrate rich diet, but now a follow up study needs to be conducted with a more balanced sex

ratio in the sample group, and which is aimed explicitly at determing if males actually select diets that are even more carbohydrate rich than that of the females.

5.3 Where do Tree Wētā Primarily Forage?

The results of the faecal fragment analysis indicated that there is a high likelihood that *H. thoracica* forage more often on the forest floor than has previously been recognised. This could be explored with a tracking study. Tree wētā galleries could be located in the wild, or artificial refuges could be attached to trees. Once colonised, the movement patterns of the inhabitants could be followed either by filming them, or if cameras are not practical, a stain and tracking paper could be used to track the direction of their nightly movements. If the study were performed in captivity, then other elements could also be factored into the analysis such as whether condition/body fat affects how frequently they forage, or whether the smell of vertebrate predators alters how they forage. Identifying where tree wētā actually go to forage, and if the presence of predators affects their normal foraging behaviour, would provide data on means by which introduced mammalian predators might impact tree wētā other than by direct predation.

5.4 What Influence do Plant Toxins Have on Tree Wētā Foraging Strategies?

Many plants produce toxic secondary metabolites to deter herbivorous foragers from consuming them, and toxic plant secondary metabolites strongly influence the feeding behaviour of most leaf-eating generalists, and therefore, probably also factor into the foraging decisions of *H. thoracica* and other wētā. In the wild generalist-herbivores can reduce the detrimental effects of toxic plant metabolites via diet balancing (feeding on a variety of plants). In the fragment analysis (Chapter 2) some highly abundant plants, such as *B. tawa*, appeared to be completely avoided by foraging *H. thoracica*, and plant metabolites may be a contributing factor in this selective aversion. Determining how the presence of a toxic substance alters the prioritisation of carbohydrates, and whether variety increases the palatibility of food items containing a toxin, would increase our understanding of the factors that influence dietary selection in tree wētā.

5.5 Does Food Size Affect Handling Time by Tree Wētā?

During the course of the nutrient study, I observed an adult male wētā eating a lyophilised food cube, off of which a number of smaller fragments had broken. While eating, one of the wētās palps touched the smaller fragments, and it discarded the larger cube to eat the smaller pieces, which it could take into its mouth whole. This raised the question whether it would be better, when performing experiments like this one, to fracture the cubes before presenting them to the subjects, rather than giving the cubes to them whole. If smaller pieces are handled more easily, and consumed more rapidly, it could lead to higher levels of consumption, and different results overall. A captive nutritional analysis could be performed with tree wētā, or potentially another orthopteran, do determine whether the state of the food cube had a signifcant effect on consumption and utilisation parameters.

6 Chapter 6: Synthesis and Closing Remarks

6.1 Synthesis

Tree wētā are insects that are endemic to New Zealand and are one of the iconic symbols of the indigenous fauna of this country. There are seven recognised species distributed throughout the North and South Islands, and *Hemideina thoracica* is the most widely distributed species of tree wētā in the North Island. Despite this, many aspects of the functional ecology of this species have not been investigated thoroughly, but this thesis has partially addressed the lack of information concerning the diet and ecology of *H. thoracica*.

Fragment analysis of the diet of *H. thoracica* in the wild revealed that their natural diet is dominated by leaves, fruits and seeds from a wide variety of native plants, but that they frequently consume other insects too, and protein derived from other invertebrates is a smaller, but potentially important component of their overall diet. Some plants appear to be consumed readily, and were present in the frass of many tree wētā from multiple areas, but other plants that were even more abundant in the same areas were frequently not present in the frass, even when the abundance was so great that it was highly unlikely that the *H. thoracica* were not encountering them. This indicates that *H. thoracica* are selective feeders. Many of the plants that the wētā appeared to be eating had relatively high concentrations of lipids and oils in their leaves compared to plants that they rejected, and the lipid and oil concentration may be a significant factor in determining the palatability of a plant to foraging tree wētā. Additionally, it appears probable that *H. thoracica* may forage on the ground more than has been previously recognised.

The image of the wild diet of *H. thoracica* that was produced in the faecal fragment analysis, was supported by the results of the nutrient balancing study. The *H. thoracica* in this study were fed on artificial diets with variable ratios of protein to carbohydrates. The choice group was able to compose its own diet from two blocks that were individually nutritionally incomplete, and this group demonstrated a strong ability to balance their intake of protein and carbohydrates. They preferentially consumed a carbohydrate rich diet, which indicates that their natural, optimal diet is composed primarily of plant materials. The digestibility of the diets was lowest in the high protein groups, but conversion efficiency (into biomass) was significantly associated with the protein concentration of the diet,

and increased dramatically from the lowest to the highest protein diets. While they strongly regulate their protein consumption, having a high conversion efficiency for protein means that wild tree wētā could grow faster, or lay down greater energy reserves by opportunistically consuming other insects for protein, when they have the opportunity to do so.

Though the wild diet of *H. thoracica* was found to include a significant quantity of fruit and seeds derived from various plants (10.4 % – 28.3 % of all fragments counted, depending on the area), it does not appear that they eat these food items in a manner that would facilitate any sort of mutualistic, co-evolutionary interaction. *Hemideina thoracica* preferentially consumed the flesh of the fruits, and frequently ignored the seeds. They often ate around the seed without moving them, and even when very small seeds were consumed, they were always destroyed in the process. In order for an animal to be a disperser, it needs to be able to pass enough seeds intact through its digestive tract to outweigh the cost of the seeds that are destroyed, and the dispersal ability of the animal needs to be greater than the distance that the seed could potentially travel by gravity or water. *Hemideina thoracica* do not appear to meet these criteria as they destroy too many seeds, and have low nightly dispersal rates. Therefore, *H. thoracica* are seed predators, and interactions between *H. thoracica* and fleshy fruit producing plants probably range from commensal to antagonistic, depending on the level of impact that seed loss has on the reproductive fitness of the plant. Tree wētā may still have a significant influence on recruitment and succession in forest ecosystems by devouring and destroying the most abundant seeds on the forest floor. In this manner they could promote species diversity by preventing a small number of highly fecund plants from pushing out other species.

6.2 Closing Remarks

Hemideina thoracica inhabit many nutritionally diverse habitats across their range in the North Island. Their well-developed ability to balance their consumption of macronutrients enables them to construct an acceptable diet from a combination of individually incomplete food sources via selective feeding strategies, and it appears likely that they preferentially forage on lipid rich foliage where possible. As large bodied invertebrates and omnivores, they are both primary consumers, and secondary consumers, converting both plant materials and protein from

smaller invertebrates into biomass, which is then available in a highly digestible form to the higher trophic-level feeders that eat tree wētā. In this way they are involved in the upwards migration of energy to a variety of endemic vertebrates, and facilitating large, stable populations of tree wētā would be beneficial to the animals which feed on them. For this purpose, I suggest that the concentration of lipids and oil glands in the leaves of the plants should be one of the factors that are considered when determining the final community composition of restoration plantings. Tree wētā appear to selectively consume these plants, and so it is likely that they are superior food sources where the tree wētā are concerned, and promoting robust populations of tree wētā would benefit the vertebrate component of the system, and thereby promote greater biodiversity in New Zealand.

7 Appendices

7.1 Appendix 1.1. Identifying *Hemideina*

Species	Pronotum Description
H. maori	Alternate dark and pale transverse bands (with no midline expansion of the dark bands).
H. femorata	Alternate dark and pale transverse bands with a midline expansion of the dark bands, dark bands are still separated at the midline.
H. crassidens	Dark bands are merged at the midline. Background colour of the pronotum is dark.
H. trewicki	Dark bands are merged at the midline. Background colour of the pronotum is pale.
H. broughi	Almost even abdominal colouration with slightly darker posterior bands, pronotal bands are nearly the same colour as the pronotum.
H. ricta	Almost even abdominal colouration with slightly darker posterior bands, pronotal bands are darker than the pronotum.
H. thoracica	Abdominal colouration is even, posterior bands are lighter. Background colour of pronotum is lighter than pronotal bands.

7.2 Appendix 1.2. The Conservation Status of Threatened Wētā, in Order of Greatest Urgency for Management Action (Sherley, 1998).

Urgent recovery work
Middle Island tusked wētā (*Motuwētā isolata*)
Wētāpunga (*D. heteracantha*)
Central Otago ground wētā (*Hemiandrus sp.*)
Short term recovery work
Mahoenui wētā (*Deinacrida n.sp.*)
Mt Faraday giant wētā (*Deinacrida n.sp.*)
Banks Peninsula tree wētā (*Hemideina ricta*)
Northland tusked wētā (*Hemiandrus monstrosus*)
Medium term recovery work
Poor Knights cave wētā (*Gymnoplectron giganteum*)
Poor Knights giant wētā (*D. fallai*)
Species about which little is known
Herekopare (or Foveaux Strait) giant wētā (*D. carinata*)
Low priority species secure in the medium term
Nelson alpine giant wētā (*D. tibiospina*)
Cook Strait giant wētā (*D. rugosa*)

Kaikoura giant wētā (*D. parva*)
Bluff (Mt Somers) giant wētā (*Deinacrida n.sp*.)
Mt Cook giant wētā (*Deinacrida n.sp.*)

7.3 Appendix 2.1: Vegetation Composition of The Study Site

A) The mean Coverage (%) of Every Plant Species, Per Tier, at the Terrace

Plant Species recorded at the terrace	% of plots with this species	Mean Cover (%) T1	Mean Cover (%) T2	Mean Cover (%) T3	Mean Cover (%) T4	Mean Cover (%) T5	Mean Cover (%) T6	Mean Cover (%) T7
B. tawa	70	2.5	2.5	2.5	0.5	1.5	1.5	0.0
B. filiforme	10	0.0	0.0	0.0	0.0	0.5	0.5	0.0
B. novaezelandiae	30	0.0	0.0	0.0	0.0	0.0	2.7	0.0
C. hastatum	20	0.0	0.0	0.0	0.0	0.0	0.0	0.6
C. rotundifolia	80	0.0	0.0	0.0	22.5	23.0	12.1	0.0
C. robusta	20	0.0	0.0	0.0	5.0	5.0	1.0	0.0
C. dealbata	70	0.0	0.0	0.0	7.5	11.5	5.5	0.0
D. cupressinum	30	10.0	10.0	7.5	1.5	1.5	1.5	0.0
D. dacrydioides	30	17.5	12.5	7.5	1.5	1.5	1.5	0.0
H. arboria	50	0.0	0.0	0.0	2.5	3.5	1.6	0.0
K. excelsa	10	0.0	0.0	0.0	0.0	0.5	0.1	0.0
L. sinense	100	0.0	0.0	15.0	65.0	54.0	40.0	0.0
L. calicaris	50	0.0	0.0	0.0	0.0	0.0	0.9	0.0
Melicytus	50	0.0	0.0	0.0	2.5	12.5	6.5	0.0
M. vimineum	20	0.0	0.0	0.0	0.0	0.0	5.0	0.0
N. cunninghamii	20	0.0	0.0	0.0	0.0	0.0	0.1	0.0
P. corymbosa	30	0.0	0.0	0.0	2.5	5.5	5.5	0.0
P. eugenioides	10	0.0	0.0	0.0	0.0	2.5	0.5	0.0
P. totara	80	12.5	10.0	11.7	7.5	5.1	4.7	0.0
P. taxifolia	80	55.0	45.0	33.0	11.5	7.6	3.6	0.0
P. crassifolius	20	0.0	0.0	0.0	0.0	0.5	0.2	0.0
P. serpens	20	0.0	0.0	0.0	0.0	0.0	0.0	1.0
R. sapida	80	0.0	0.0	0.0	0.0	0.3	7.2	0.0
Selaginella	40	0.0	0.0	0.0	0.0	0.0	20.0	0.0

B) The mean Coverage (%) of Every Plant Species, Per Tier, at the Mid Hillslope

Plant species recorded at the mid hillslope	% of plots with this species	Mean Cover (%) T1	Mean Cover (%) T2	Mean Cover (%) T3	Mean Cover (%) T4	Mean Cover (%) T5	Mean Cover (%) T6	Mean Cover (%) T7
A. cunninghamii	20	0.00	0.00	0.00	0.00	0.00	0.60	0.00
A. flaccidum	20	0.00	0.00	0.00	0.00	0.00	0.10	0.50
A. oblongifolium	20	0.00	0.00	0.00	0.00	0.00	2.50	3.00

B. tawa	60	7.50	22.50	17.50	11.00	2.50	2.60	0.00
B. chambersii	10	0.00	0.00	0.00	0.00	0.00	2.50	0.00
B. filiforme	30	0.00	0.00	0.00	0.00	0.00	15.00	0.00
B. fluviatile	10	0.00	0.00	0.00	0.00	0.00	0.00	2.50
B. repens	10	0.00	0.00	0.00	0.30	0.20	0.20	0.00
C. serratus	40	0.00	0.00	0.00	5.00	3.10	3.60	0.00
C. dealbata	90	0.00	0.00	5.30	47.50	35.50	19.10	0.00
C. medullaris	20	0.00	0.00	10.00	7.50	1.00	1.00	0.00
C. hastatum	10	0.00	0.00	0.00	0.00	0.00	0.00	0.50
C. robusta	10	0.00	0.00	0.00	0.00	0.10	0.10	0.00
C. rotundifolia	50	0.00	0.00	0.00	2.50	10.10	3.60	0.00
C. spathulata	20	0.00	0.00	0.00	0.00	2.50	0.60	0.00
D. cupressinum	20	7.50	7.50	5.00	1.00	1.00	1.00	0.00
D. dacrydioides	30	10.00	10.00	7.50	1.50	1.50	1.50	0.00
D. fibrosa	30	0.00	0.00	12.50	7.50	1.50	1.50	0.00
G. ligustrifolium	30	0.00	0.00	0.00	5.00	3.00	3.00	0.10
H. arboria	20	0.00	0.00	0.00	0.00	0.00	0.60	0.00
Hymenophyllum	10	0.00	0.00	0.00	0.00	0.00	0.50	0.00
K. excelsa	30	0.00	0.00	0.00	0.00	0.00	1.58	0.00
K. ericoides	30	0.00	5.00	10.00	7.50	3.50	1.50	0.00
L. sinense	70	0.00	0.00	7.50	7.50	13.00	10.70	0.00
L. calicaris	60	0.00	0.00	0.00	0.00	1.00	1.70	0.00
Melicytus	50	0.00	0.00	3.00	8.00	13.50	11.00	0.00
M. diffusa	50	0.00	0.00	0.00	0.00	0.00	3.10	7.60
M. vimineum	10	0.00	0.00	0.00	0.00	0.00	5.00	0.00
M. pustulatum	50	0.00	0.00	0.00	0.00	0.00	2.60	10.50
M. australis	40	0.00	0.00	0.00	5.00	5.50	3.60	0.00
N. cunninghamii	60	0.00	0.00	0.00	0.00	0.00	2.80	0.00
Parsonsia	10	0.00	0.00	0.00	0.00	0.00	0.00	0.50
P. corymbosa	50	0.00	0.00	0.00	0.00	6.50	6.10	2.50
P. trichmanoides	20	0.00	0.00	0.00	0.00	0.10	0.10	0.00
P. totara	30	0.00	15.00	12.50	5.50	1.50	1.50	0.00
P. taxifolia	40	20.00	17.50	12.50	8.00	4.00	2.00	0.00
P. crassifolius	40	0.00	0.00	0.00	0.00	1.00	0.80	0.00
R. sapida	30	0.00	0.00	0.00	0.00	0.50	1.10	0.00
R. scandens	30	0.00	0.00	0.00	0.00	0.00	0.00	3.50
V. lucens	10	0.00	0.00	0.00	0.50	0.50	0.50	0.00

C) The mean Coverage (%) of Every Plant Species, per Tier, at the Upper Hillslope

Plant species recorded at the upper hillslope	**% of plots with this species**	**Mean Cover (%) T1**	**Mean Cover (%) T2**	**Mean Cover (%) T3**	**Mean Cover (%) T4**	**Mean Cover (%) T5**	**Mean Cover (%) T6**	**Mean Cover (%) T7**
B. Tawa	30	25.00	25.00	16.67	6.11	3.89	1.67	0.00
B. filiforme	30	0.00	0.00	0.00	0.00	0.00	6.11	0.00

C. serratus	30	0.00	0.00	0.00	5.00	3.50	1.50	0.00
C. dealbata	80	0.00	0.00	5.00	20.00	25.00	16.00	0.00
C. medullaris	10	0.00	0.00	2.50	2.50	0.50	0.50	0.00
C. hastatum	20	0.00	0.00	0.00	0.00	0.00	0.00	3.00
C. rotundifolia	30	0.00	0.00	0.00	7.50	5.50	3.50	0.00
C. spathulata	10	0.00	0.00	0.00	0.00	0.00	0.60	0.00
G. ligustrifolium	50	0.00	0.00	0.00	7.50	8.50	4.50	0.00
Hymenophyllum	10	0.00	0.00	0.00	0.00	0.00	0.50	0.50
K. excelsa	50	2.50	2.50	0.00	0.00	8.00	8.60	0.00
K. ericoides	60	0.00	12.50	25.00	20.00	9.50	5.50	0.00
L. sinense	30	0.00	0.00	0.00	3.00	3.00	3.60	0.00
L. calicaris	80	0.00	0.00	0.00	8.50	4.50	5.20	0.00
M. ramiflorus	10	0.00	0.00	0.00	0.00	0.00	2.50	0.00
M. ramiflorus	90	0.00	0.00	0.00	13.50	14.00	8.10	0.00
M. pustulatum	50	0.00	0.00	0.00	0.00	0.00	12.60	5.00
M. vimineum	40	0.00	0.00	0.00	0.00	0.00	13.00	0.00
M. australis	50	0.00	2.50	2.50	5.50	6.50	6.80	0.00
P. totara	100	5.00	51.50	37.50	20.00	6.50	6.50	0.00
P. taxifolia	20	0.00	0.00	0.00	0.00	0.00	0.60	0.00
P. crassifolius	30	0.00	0.00	0.50	3.00	5.50	2.00	0.00
P. serpens	50	0.00	0.00	0.00	0.00	0.00	0.00	4.00
R. sapida	70	0.00	0.00	0.00	0.00	0.00	1.90	0.00
R. scandens	20	0.00	0.00	0.00	0.00	0.00	0.00	7.50
Selaginella	40	0.00	0.00	0.00	0.00	0.00	20.00	0.00
T. officinale	10	0.00	0.00	0.00	0.00	0.00	0.50	0.00

7.4 Appendix 2.2 Chi Squared of Consumption vs. Availability

A) Expected vs. Observed Frequencies of Fragments at the Terrace

Plant species	Recorded Ground Cover (%)	Adjusted Ground Cover (%)	Expected counts	Observed counts
C. hastatum	5	2	457	0
C. rotundifolia	16	7	1467	868
C. dealbata	7	3	635	23
D. cupressinum	7	3	631	111
D. dacrydioides	14	6	1270	4377
L. sinense	58	26	5300	790
Melicytus	13	6	1142	2227
M. vimineum	5	2	457	0
P. corymbosa	6	2	503	809
P. totara	13	6	1142	648
P. taxifolia	55	25	5026	5346
R. sapida	7	3	658	4
Selaginella	20	9	1828	0

B) Expected vs. Observed Frequencies of Fragments at the Mid Hillslope.

Plant species	Recorded Ground Cover (%)	Adjusted Ground Cover (%)	Expected Counts	Observed Counts
B. tawa	23	9	1162	0
B. filiforme	15	6	775	0
C. serratus	5	2	258	0
C. rotundifolia	10	4	522	256
C. dealbata	48	19	2453	312
C. medullaris	10	4	516	0
D. cupressinum	8	3	387	210
D. dacrydioides	10	4	516	465
D. fibrosa	13	5	645	0
G. ligustrifolium	5	2	258	0
K. ericoides	10	4	516	1709
L. sinense	13	5	671	56
Melicytus	16	6	800	1616
M. diffusa	8	3	392	0
M. vimineum	5	2	258	0
M. pustulatum	11	4	542	0
M. australis	6	2	284	125
P. corymbosa	7	3	336	89
P. totara	15	6	775	1820
P. taxifolia	20	8	1033	537

C) Expected vs. Observed Frequencies of Fragments at the Upper Hillslope

Plant species	Recorded Ground Cover (%)	Adjusted Ground Cover (%)	Expected counts	Observed counts
B. tawa	25	10	1645	0
B. filiforme	6	2	402	0
C. serratus	5	2	329	811
C. rotundifolia	8	3	494	181
C. dealbata	25	10	1645	6
G. ligustrifolium	9	3	559	0
K. excelsa	9	3	566	0
K. ericoides	20	8	1316	3497
L. calicaris	9	3	559	0
Melicytus	17	7	1086	1
M. pustulatum	13	5	829	0
M. vimineum	13	5	856	0
M. australis	7	3	448	2
P. totara	51	21	3356	5475
P. crassifolius	6	2	362	15
R. scandens	8	3	494	0
Selaginella	20	8	1316	0

7.5 Appendix 3.1. Weight Gain, Dry Weight Consumed, and Performance Indices for all Groups

Group 1	Total Consumed (g)	Con Rate (g/d)	Total Growth (g)	Growth Rate (g/d)	Total Frass (g)	AD (%)	ECD (%)
1 (F)	0.19	0.01	0.04	0.00	0.02	89.54	24.59
2 (F)	0.32	0.01	0.04	0.00	0.08	76.43	16.96
3 (F)	0.34	0.01	0.36	0.01	0.09	74.05	145.02
4 (F)	0.25	0.01	0.03	0.00	0.01	94.52	12.65
5 (M)	0.65	0.02	0.17	0.01	0.07	89.79	28.86
6 (M)	0.54	0.02	0.00	0.00	0.07	87.55	0.43
7 (F)	0.33	0.01	0.00	0.00	0.05	84.24	0.69
8 (F)	0.41	0.01	0.22	0.01	0.03	93.62	57.03
9 (F)	1.23	0.04	1.01	0.03	0.20	83.54	97.73
Means	0.47	0.02	0.21	0.01	0.07	85.92	42.66
Group 2	**Total Consumed (g)**	**Con Rate (g/d)**	**Total Growth (g)**	**Growth Rate (g/d)**	**Total Frass (g)**	**AD (%)**	**ECD (%)**
1 (F)	0.51	0.02	0.19	0.01	0.10	81.34	45.15
2 (M)	0.55	0.02	0.20	0.01	0.10	82.07	45.11
3 (M)	0.47	0.02	0.20	0.01	0.05	90.39	46.96
4 (F)	0.46	0.02	0.19	0.01	0.07	84.56	48.87
5 (F)	0.88	0.03	0.47	0.02	0.21	76.43	69.83
6 (M)	0.27	0.01	0.04	0.00	0.02	92.09	14.31
7 (F)	0.65	0.02	0.28	0.01	0.11	82.88	51.42
Means	0.54	0.02	0.22	0.01	0.09	84.25	45.95
Group 3	**Total Consumed (g)**	**Con Rate (g/d)**	**Total Growth (g)**	**Growth Rate (g/d)**	**Total Frass (g)**	**AD (%)**	**ECD (%)**
1 (F)	0.22	0.01	0.06	0.00	0.03	88.47	32.67
2 (F)	0.78	0.03	0.08	0.00	0.20	74.90	13.93
3 (M)	0.61	0.02	0.22	0.01	0.15	75.83	46.54
4 (F)	0.18	0.01	0.08	0.00	0.02	86.84	55.25
5 (F)	0.44	0.01	0.37	0.01	0.09	79.51	106.67
6 (M)	0.59	0.02	0.45	0.02	0.10	83.49	91.36
7 (F)	1.19	0.04	0.85	0.03	0.30	74.65	95.78
8 (F)	0.57	0.02	0.62	0.02	0.11	80.80	133.74
9 (F)	0.84	0.03	0.48	0.02	0.24	71.17	80.19
Means	0.60	0.02	0.36	0.01	0.14	79.52	72.90
Group 4	**Total Consumed (g)**	**Con Rate (g/d)**	**Total Growth (g)**	**Growth Rate (g/d)**	**Total Frass (g)**	**AD (%)**	**ECD (%)**
1 (F)	0.36	0.01	0.33	0.01	0.08	77.84	120.09
2 (M)	0.39	0.01	0.34	0.01	0.09	76.51	112.81
3 (M)	0.62	0.02	0.33	0.01	0.13	79.57	67.95
4 (F)	0.50	0.02	0.50	0.02	0.14	71.81	139.41
5 (M)	0.54	0.02	0.13	0.00	0.12	77.02	32.36
6 (F)	0.45	0.02	0.27	0.01	0.11	74.99	80.47
7 (F)	0.31	0.01	0.11	0.00	0.04	87.47	39.04
8 (F)	0.73	0.02	0.81	0.03	0.22	69.74	158.14
9 (M)	0.45	0.02	0.37	0.01	0.09	79.90	101.90
Means	0.48	0.02	0.36	0.01	0.11	77.20	94.69

7.6 Appendix 4.1: The Sex, Weight, and Head Width of all *H. thoracica* used in the Seed Eating Trial.

Wētā Number	**Sex**	**Weight (g)**	**Head Width (mm)**
1	M	2.83	8.45
2	M	1.29	6.3
3	M	1.39	6.79
4	M	3.87	11
5	M	1.24	6.15
6	M	2.53	9.4
7	M	1.92	7.37
8	M	2.42	7.15
9	M	1.31	6.45
10	M	1.27	6.98
11	M	3.30	10.71
12	M	2.29	7.43
13	M	1.24	6.29
14	M	1.40	6.58
15	M	2.70	10.07
16	F	3.68	7.74
17	F	3.36	7.13
18	F	4.09	7.35
19	F	2.56	6.22
20	F	3.61	7.84
21	F	4.20	7.02
22	F	3.08	6.96
23	F	3.98	7.34
24	F	4.21	7.49
25	F	3.45	6.9
26	F	3.70	7.45
27	F	1.91	6.25
28	F	3.55	7.73
29	F	3.87	7.3
30	F	2.59	5.33
31	F	4.58	7.38
32	F	3.96	7.25
33	F	1.78	6.05
34	F	3.65	7.77
35	F	3.37	7.3
36	F	3.11	7.84
37	F	3.48	7.66
38	F	3.65	7.44
39	F	3.57	7.61
40	F	4.14	6.9

7.7 Appendix 4.2: The Length, Width, and the Average Number of Seeds in *C. repens*, *C. australis*, and *F. procumbens* Fruit.

	Mean (mm)	95% Conf.limit (mm)
C. repens Berry Length	8.4	0.3
C. repens Seed Length	6.6	0.3
C. repens Seed Width	3	0.2
C. repens Seed Number	2	0
C. australis Berry Length	4.6	0.3
C. australis Seed Length	2.7	0.1
C. australis Seed Width	1.5	0.2
C. australis Seed Number	6.7	2.6
F. procumbens Berry Length	14.1	1
F. procumbens Seed Length	1.9	0.1
F. procumbens Seed Width	1	0.1
F. procumbens Seed Number	72.4 (18.1/locule)	16.8

Thank You

Male *H. thoracica* inside a privet. Photo by Author (2013).